Seams in the Mist

Population Differentiation along Environmental Gradients in Four Dipterocarpaceae Blume Species, and their Extended Foliar Phenotypes

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For Carolina,

I imagine a good world,
in which

your naïve memory,
sweet and aloof in me,
moves alee, and
pleases fluently,

Then cruelty; my grief ruins me.

Let me stay sane, I pray,
as I delay the pain away.

“Let us be famous, we relatives, for our journeying.
Do not let us die,
do not let us go short of breath,
It is good how we relatives talk with each other,
good the affection we relatives share with each other,
as we go to sleep in this jungle shelter.”

(Excerpt from a Sarawak Dayak prayer for journeying to find a new home [tivai tai buau]; Rubenstein 1985:279)

Abstrak

Tumbuh-tumbuhan hutan hujan tropika menunjukkan perbezaan genetik molekular yang ketara merentasi skala ruang yang agak kecil secara relatif. Walau bagaimanapun, implikasi perkara ini terhadap ekologi fungsian masih kurang difahami. Bagi mengisi kekosongan ini, buah-buahan daripada progeni liar empat spesies Dipterocarpaceae Blume telah dikumpul dan ditanam sebagai anak pokok di sebuah kebun am di Sabah, Malaysia. Selepas kira-kira dua setengah tahun, ciri-ciri fungsian dan komuniti daun yang berkaitan telah diinventori, dan pengaruh genetik dan persekitaran telah diteliti.

Ketinggian pokok induk dan tanah mempengaruhi ciri-ciri anak pokok dalam keempat-empat spesies. Secara khususnya, pertumbuhan ketinggian dan diameter, jumlah dan keluasan daun spesifik, serta kandungan klorofil, P, dan K pada daun ditentukan secara genetik. Semua ekspresi ciri ini turut dipengaruhi oleh persekitaran, yang secara amnya, memberikan pengaruh yang lebih besar daripada warisan genetik.

Tambahan pula, variasi dalam struktur komuniti daun ditentukan secara genetik dalam satu spesies: *Shorea johorensis* Foxw. Ini adalah penemuan baharu yang meluaskan kajian fenotip lanjutan ke kawasan tropika lembap. Tambahan, dalam keempat-empat spesies terdapat kekangan ciri yang bererti terhadap struktur komuniti, yang ekspresinya ditentukan secara genetik dalam tiga daripadanya. Laluan penuh pengaruh genetik terhadap ekspresi ciri anak pokok dan struktur komuniti daun, kepada pengaruh-ciri terhadap komuniti tersebut diperhatikan dalam *S. johorensis*.

Penemuan ini penting untuk operasi pemulihan hutan yang bergantung pada penempatan dan pemilihan anak pokok, tetapi juga untuk pemuliharaan kepelbagaian genetik di hutan hujan tropika, memandangkan ancaman baharu semakin meningkat. Pemilihan anak pokok secara pra-penyesuaian yang menunjukkan kombinasi ciri yang menguntungkan mungkin mengehadkan kehilangan kecergasan berkaitan dengan perubahan iklim, baik dalam populasi dipterokarpa mahupun komuniti daunnya. Oleh itu, output pengurusan dapat ditingkatkan.

Kata kunci: Borneo, ciri fungsian pokok, Dipterocarpaceae, ekologi hutan hujan tropika, evolusi, fenotip lanjutan, genetik tumbuhan, kepelbagaian biologi, percubaan progeny, spektrum ekonomi tumbuhan

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Abstract

Tropical rainforest trees show strong molecular genetic differentiation across relatively small spatial scales. The implications of this for functional ecology are poorly understood however. In order to fill this vacancy, fruits from wild progeny of four species of Dipterocarpaceae Blume were collected and planted as seedlings in a common garden in Sabah, Malaysia. After approximately two and a half years, functional traits and associated foliar communities were inventoried, and genetic and environmental influences investigated.

Mother tree elevation and soil influenced seedling traits in all four species. Specifically, height and diameter growth, total and specific leaf areas, and foliar chlorophyll, P, and K contents were genetically determined. And all these trait-expressions were additionally conditioned by the environment, which, generally, exercised greater influence than genetic heritage.

Furthermore, variation in foliar community structure was genetically determined in one species: *Shorea johorensis* Foxw. This is a novel discovery expanding the study of extended phenotypes to the humid tropics. In all four species, additionally, there were significant trait-constraints on community structure, whose expressions were genetically determined in three of them. Full pathways from genetic influence on seedling trait expression and foliar community structure, to trait-influence on these communities was observed in *S. johorensis*.

These findings are significant for restoration operations relying on seedling deployment and selection, but also for the conservation of genetic diversity in tropical rainforests, as novel threats amplify. Pre-adaptively selecting seedlings expressing favorable trait-combinations might limit fitness-loss related to climate change, both in dipterocarp populations and their foliar communities. Therefore improving management outputs.

Keywords: biodiversity, Borneo, Dipterocarpaceae, evolution, extended phenotype, plant economic spectrum, plant genetics, progeny trial, tree functional traits, tropical rainforest ecology

Prologue

How the spirit sings

Stretching of the cotyledon

Something beautiful emerges through rhyme, whose cause has, to me, not quite condensed yet. I would claim it not to be enough to simply juxtapose two similar-sounding words, as any random jumble of rhyme or assonance, then, must suffice. And this, they would not under the logic of reason; the infinite battle against stochastic entropy. The beauty in rhyme needs creativity—some meaningful interaction in the pairing is demanded. Thus, two dimensions of rhyme have been identified: vocalization – as the physical property that finds rhythm in sound – and spirit – as the meaning behind the vocals, extending them into beauty. Both are necessary. The spirit of the author picks patterns out of seas of noise, plays with structure, imbues them with meaning, and coerces stagnant frequency into experience. Our relation to their inherent symbolism, say through language, extends strings of letters into poetry, whose transcension remains impossible without the physical. As its vocalization roots the poem in soil, its spirit raises cotyledon out of subterranean ontic entropy, and the gusts of life imbues their inertia with beauty.

The physical sciences – physics, chemistry, biology – record the vocalizations of nature, filling the ocean of noise for the spirit to fish. Carbohydrate metabolism, volatile compound bouquets, gibbon calls in the jungle—traits and processes of all conceivable degrees of triviality. As such, their theories are essential, though not sufficient, for an experience of natural beauty. During failed attempts to reduce it to the physical properties any of these sciences measure, all frauds must recognize the impossible task of rejecting the sensible faculties involved with the hypothesized "less favorable" impressions, and weave what biological automaton assembles the most valuable aesthetic products. These tasks are not made impossible entirely by physical limitation – though they might be partly –, but because they require a solution to the issue of hierarchy in utility, and so uniformity in the axes of qualities of things. No mathematical weight will emancipate this prisoner if one single sensible impression remains non-reducible. This fraud would, without hesitation, have to claim not only that this or that is beautiful, but by how much; they would have to quantify the beauty in the color magenta, and deduce its triumph or defeat over the smell of tar. Which properties are the most desirable? What weft of our faculties assembles the most valuable aesthetic products, thus demanding our non-divisible attention? Is it our eyes or ears, our skin and tongue? Where are then the industrialized perfected forms, unimpressed by culture, to which all succumb, which we must assume to exist under the coercion of capitalized employ? They *are* not. Taste is not ubiquitous; as creativity embodies the path of spiritual exploration, all true composers and painters and poets endlessly renew their senses and dream of beauty. The assumption of homogeneity across the dimensions of being fails to account for creativity, and is not congruent with aesthetic experience.

Already, then, we encounter opposition against the ignorance of spirit. And once subjectivity in experience is accounted for, we see this reduction as decisively impossible. Would your aesthetic hierarchy differ from mine? Even slightly? This could not be. Not only would the qualities in physical objects have to be uniformly comparable without loss, but their observation require independence of the observer. Additionally, phenomenal experience would be assumed to be non-contingent on broader biological make; there would be no distinction between human and non-human experience. Perhaps only the magnitude of sensory observation, as the summed spectra of all units of property any one being's senses recognizes, could approximately differentiate any two species of individuals, because all observation of any particular set of information of any quality would have to be uniform. We are dooming aesthetics into anthropology. And so, its reduction to the material requires homogeneous being and insight into what no one can ever know: what it is like to be what they are not. All experience of all material property become exactly equal, and all subjects the same; no individuals are left, only their mass in space. This position demands the deterioration of ontology through the entropic pooling of beings—loss of will.

The genesis of beauty will not be found in material, but in experience—its synthesis with being. Within elucidated interactions affirming transgressive existential dependency. If not, woe unto whoever, under the misguided presumptions of some physical reductionism, fails to experience continuous euphoria in the presence of the most mundane and horrid traits of the world: the homogeneity of sun-bleached empty parking lots, deafening hums of waiting room ambience, the smell of rotten carrion, cries of terror, taste of gastropod mucus, conversion of tropical rainforest into garbage dump, a sea of plastic waste in the Pacific Ocean, or marine genocide. The pleasantness in color or smell of oil spills matters nothing when juxtaposed with its associated violation of marine life. Only deafness and inverted vision, in aggregate, retain a rightful claim to such inference. When eyes open and the soul awakens, only, will the breadth and breath of the world yield transgressive paradigms and make explicit the beauty of the world. Because its limits are not confined within anthropology.

So praise our spirits! The saviors of this hell; the unit that separates me from you and makes us unique; the engine of being; the will that stretches the cotyledon that catches the wind. Gases and volatile compounds knock on the guard cells of its stomata, who open and close at the behest of their ratios. A complex of metabolism is induced, whose subsequent sludge suspends into the causal mysteries of spirit, which respond through governance of the body and its movement towards purpose.

When formative mechanisms of soil and weather coerce its body, the spirit of the jungle tree embryo is primed into self-recognition and initiates its toil of meaning. Through incommensurably intricate wefts of mechanical complexity, laboring in the processes transforming the heavily weathered acrisols of the remnants of the Sunda into flourishing compositions of self-sustaining cycles of death and rebirth. Ecdysis of acid bedrock; life molting its abiotic chrysalis, giving temporary form to the infinitely creative machinations of evolution. In lapping waves, weaving an eternally expanding tapestry of interacting being. At its own behest, life, as its purpose, yields itself through the domestication of mineral rock and sour monsoon. The world whispers and spirits of stretched cotyledon sing in rhyme.

Ode to the heart and its death

Does some naivety corrupt the constitution of my volition? Ought I simply look for momentary pleasure without dependency? Then, what if any such attempts continuously fail to yield any sense out of my experienced meaning? What if my spirit, on its own grounds, rejects these volatile vassals? What if its maintenance requires enduring intimacy? I *want* it… no—I *crave* it. In fact, who could deny *it—love*? I *need* to love someone who *needs* to love me. And what, then, would be the purpose of reducing such a volition – of existence – to idealism? The framework through which the pragmatic chooses to determine their hypotheses, degenerates into nihility when my soul demands something of me—when the fabric of its motion weaves my being. When it is felt, whoever claims love to be the purpose of the heart is no idealist, but an empiricist. They have simply acknowledged and accepted its absurd notion and significance. Without jurisprudence; no requirement for a rational defense phases them. Humbled honesty. The absence of this inconceivable condition – *true love* – summons the lonely spirit, its scant supply an existential persistence; none but poetry the embrace of, both, its melancholia from demand and beauty in supply, in contiguity.

In throbbing motion, a vector of being forms entirely unique knots as their hearts are guided by the economy of love—through time, weaving an infinite braid. From these aggregates, like lignin polymers, diverging strands bind the fates of collectives, which radiate in all directions of all dimensions from the singularity of time. Though their journeys between knots vary, all spirits attract all others, and so every repulsion initiates a collision. As any diaspora of molecule or spirit diverges, whether by effect or will, in short they will produce another through the volition of heart. This richer than the last. Consequently, then, spirits, through molecule, sequester another into an infinite string of purpose. Whose movement laps and leaps over the tapestry of being, of which everything is made and that which makes everything. If death only could be conceived as physical decomposition through the acceptance of nihilism by spirit, any life would realize all prior in rhyme. As my spirit embraces the abyss, my body decomposes, its material scatters, in time producing some being necessitating purpose; through transfer of molecule, what yielded my spirit and its cessation has birthed another, who continues to labor in the weft I participated. Beauty in being.

A song of the fetishization of industry

In Alnarp, the Swedish University of Agricultural Sciences maintains one of the most beautiful campuses in the world. Surrounding the lecture halls and library, trees of all kinds grow. Most notable, perhaps, behind the castle, is the old-growth oak savanna and its adjacent beech forests and ash-elm-hazel groves. Extending from this core, the park's stewards have planted untold exotic mixtures, such as American and Asian cedars (*Thuja* L. spp.), cypresses (*Chamaecyparis lawsoniana* [A.Murray bis] Parl.), birches (*Betula* L. spp.), oaks (*Quercus* L. spp.), planes (*Platanus* L. spp.), walnuts (*Juglans* L. spp.), pines (*Pinus* L. spp.), wingnuts (*Pterocarya* Kunth spp.), maples (*Acer* L. spp.), katsura (*Cercidiphyllum japonicum* Siebold & Zucc.), poplars (*Populus* L. spp.), larches (*Larix* Mill. spp.), magnolias (*Magnolia* Plum. ex L. spp.), tulip trees (*Liriodendron tulipifera* L.), and many more species of herbs and shrubs.

I have spent many hours painting trees and flowers and insects, and reading books and papers in this park. It is here I found my love for Emerson's (1836) *Nature*. My favorite spot for reading is a small cherry garden behind the library. These trees are tall enough to provide dappled shade, without being monumental and overbearing. Its shrubs provide comfortable walls, eliciting isolation, yet open enough space beneath the canopy to free my view throughout. These cherry stems form crooked, slithering, branches at eye level; their canopies encroaching right above my head; shading the ground vegetation as an organic dome. It is a miracle of horticulture. A real art of grafting—biotic manipulation. Deliberate conversion corroborating the human industrial will; violent, non-consensual coercion. As quickly as I notice the artistic effort, I mourn the deceit behind these forms and structures—the trees never made an effort to grow like this, they were forced to.

Humans moved these cherries and planes and wingnuts, half-way around the world, away from their natal environments, and doomed them into habitats their kind had never before had the pleasure to influence; no wayward parasites to inspire, no associated traveler to imbue, no caprice to exploit. No natives with habitats to colonize. Undeniably, the shapes humans are able to force nature into merit awe, but do they yield beauty? Do they yield interactive immersion and transcendence? No. They are a nuisance to native life – the interactive webs of plants, birds, fungi, nematodes and nematomorphs, bacteria, algae, mammals, protozoa, beetles, wasps and other parasitoids, mosses and lichen –, with which they share barely any recent evolutionary history. Contextualized, these cherry trees benefit no one's experience but the ignorant humans who, erroneously, consider introducing novel physical properties, such as color and shape and smell, to be the end of horticulture and natural beauty.

When structures and forms, similar to the mangled boles and crowns of the Alnarp cherry garden, develop in forests without the need for human induction, they strike us as more than revered—they are truly beautiful. I have seen multiple stems of old oak grow into each other, becoming a single unit of ancient life. And stems of pedunculate oak, Norway maple, and Scots pine interweave into a living, organic, spire. Roots of Norway spruce surviving the perils of the Scandian alps by digging into its shallow soil, reproducing stems for thousands of years; living through interglacial eons. One hundred year-old conifer logs and snags, which had lived for another four hundred years prior, providing habitat for an inconceivable amount of individuals of thousands of species of epiphytes and saprophytes and parasites. Fern nests in jungle canopy, hosting profuse densities of insects and fungi, spawning floating arboreal communities by raising the soil into the sky.

Disregarding any utilitarian aggregate arguments, these natural experiences have yielded me more beauty than any coerced configuration of color and texture could. Again, not because of the summed interactivity of all related biological lodgers – even if weighted against some hypothesized moral density –, but because their existential significance beyond my utility has been illuminated. Or, maybe rather, the independence of beauty from humanity, and therefore the infinite extent of all's purpose.

What anthropogenic coercion could possibly command mimicry of the spiral wefts of mating leopard slugs, who – through their heads – turn their gametes inside out while, entangled, dance in suspended mucous intimacy? Exposing their most vital organs, explicitly jeopardizing their hypothesized fitness to experience and display existential beauty only once before their passing. Or fractal *Cladonia* lichen thalli endowing humus strata? Which, through their mycobionts, steer mineral water, and photobionts, breath vapor into the troposphere like trachea of taiga soil. What confined sense of beauty could the human mind muster, that fragile and petite *Calypso* flowers, through magenta bloom, replicating stellar constellation aloft carpets of boreal feather moss and litter, could not? A European starling bachelor, presenting – selected – pleasantly smelling herbs for females, which are intervowen in nests, stimulating nestling immune system and inhibiting parasitic infection.

Ecology provides a terminology to express existential dependency on a system humans cannot provoke or alter, degrade or ruin; a language of obedience and the rejection of stewardship as end. A hangover-cure for greed-induced stupor, self-diagnosed supremacy, and infantilization of culture through commerce. A language of non-anthropocentric empathy and love; of acknowledged equity, in humans and all other life. This is the basis for environmental ethics—not economy, nor theology or policy. An empirical foundation for the rights of *life*.

As every physical theory either introduces or corroborates a metaphysical position, an economic theory of land-use involves itself with environmental ethics and natural ontology. Are the assumptions behind, and associated requirements for the use of, the theory congruent with empirical observation? If not, the magnitude of their discrepancies might indicate the aptness for the continuation of this status quo. What consequences are the application of a theory, which fails to account for its own indispensable conditions, and how plastic are these; how far can one's assumptions stretch before the earth beneath crumbles and hell devours their abuser? Would a torment contraction, which *will* ripple outwards waves of destruction, only providing glimpses of ecological apocalypse but not its promise, not only prevent extinction but also initiate moral sensibility for the future?

Wherever a plot of arable land there was once, most often, either a forest, grassland, wetland, or something in-between. The structures and processes that produced these systems were eventually all destroyed. Either directly through deforestation, conversion, or draining, or indirectly by coercively facilitating the same or similar degradation through other species, such as inducing transformation into alternative ecological stable states. Old and resilient mixed forests are replaced by monodominant plantations to be devoured in adolescence, deep grasslands lacerated for cereal crop, and peatlands strangled by shovel and dynamite. Ballast water and garden seedlings carry generalist scavengers and parasites across Earth. And eventually, some of these run wild, consuming wood, water, and flesh; smothering ancient trees with immunity (Davydenko et al. 2022), homogenizing diverse wetlands into degeneracy (Jacquart et al. 2005), and imbuing blood-sucking carriers of deadly disease with habitat (Mwangi & Swallow 2008).

At a rate parallelling all known prior apocalypse events, through their fetish for industry, human has extirpated and made go extinct thousands of species of trees, shrubs, herbs, lichen, fungi, beetles, butterflies, amphibians, bats, birds, fish, ungulates, cats, dogs, and primates (Ceballos et al. 2015; Cowie et al. 2022). We do not see enough resemblance in even our hominid cousins to spare them, their cultures, or development of their spirit (Kühl et al. 2019). Only the species whose industrial utility we have managed to quantify into capital are exempt. At least momentarily, until the aggregate of species they themselves utilize for survival, which we have failed to account for, disappear (Liu et al. 2022)—alongside our proposed utility. At which point our existential dependency on, through fundamental obedience to, nature must become apparent. Else our being condemns us into means of extinction. This is your last opportunity for regret; your existential singularity.

What the world whispers of

I enter the forest without fear.

I know what plants and their parts burn and sting,
    are sweet, sour, and rotten,
If I can touch them and how,
I know that these roots taste good and those flowers
    smell bad,

That swallowing this leaf might kill me,
And where others might grow and when.

I know what flowers and bushes were introduced by
    human and where from,
What life they displace and how they
    transmit disease,
That the larvae of this moth and that butterfly eat
    those herbs,
I know what tree will survive in this shade,
Which soil produces what berries,
And where to sit for rest.

I know what leaves make those noises,
That these kinds of beetles burrowed this log,
What those fungi tell of this soil,
And which bird is singing what.

Now I know that
    everything whispers, even the wind.
But I couldn't guess why.

Contents

Glossary

Allopatry	When two populations, as a cause of geographic isolation, diverge evolutionarily until they become distinct species, allopatric speciation has occurred. In evolutionary terms, geographic isolation implies disruption of gene flow due to natural barriers like mountains, rivers, or forests, etc., which only have effect if the species presents ecological sensitivity to the barrier in question.
Calciphobous	Being disfavored by calcareous conditions, e.g. limestone-rich soil.
Community	*Community ecology* is the study of groups of organisms; how populations of different species interact, how they influence each others' distributions and structure ecosystems. A *community* is therefore a collection of species representing some ecosystem.
Coverage	A measure of sample completeness. *Coverage* estimates the proportion of all species in the population a sample covered. Chao & Jost (2012) developed it as an alternative to the method of normalizing samples by size, which biases comparison when species abundances, naturally, differ a lot between populations.
Cryptic invasion	*Cryptic invasion*, here, refers to the introduction of exotic genotypes – at the cost of native genotypes – into habitats considered to be within the native range of the species. Essentially, biological invasion at smaller scales than *species*. An introduction of an exotic species, which goes unnoticed due to phenotypic similarity to a native species, can be called *cryptic* as well. Generally, then, a *cryptic* process might simply be describing some unnoticed event. Though my use of the term refers to the former definition: intraspecific biological invasion.
Dispersal	In biology, *dispersal* refers to the spatial movement of organisms. In plants, specifically, *dispersal* often

refers to either pollen or seed (fruit) *dispersal*—this is how the term is used here. Dipterocarp pollen is *dispersed* by insects (pollination), their fruits are *dispersed* by wind (gyration).

Emergent trees, and *dipterocarp forest strata*	Dipterocarp forest canopies are complex. There are many species vying for similar resources, including space. At any point in time, the layers of branches are thought of as *strata* in the canopy. Smaller trees, that either do not grow tall or are suppressed by taller trees, grow in the understorey. Above grow the trees in the sub-canopy and then the canopy layers. *Emergent trees* are trees within the *emergent* layer. These are generally (with some exception) the tallest trees in dipterocarp forests, and some of the tallest in the world. This idea of layering, or *stratification*, is the usual framework for analyzing phytosociology in forest trees. Whitmore (1998:6, 29) presents the canopy structures in two dipterocarp forests inventoried by Ashton (1964a; b).
Extended phenotype	If *phenotype* is the product of genomic expression, and genomes influence trophic interactions beyond its host body, then there are *phenotypes* that *extend* beyond the body of the expressed genome. These are known as *extended phenotypes*.
Function (ecological)	All parameters of all ecosystems change through time, at different rates. These changes depend on the consistency of the processes maintaining the ecosystem through any (short) interval of time. These kinds of “maintenance” processes can be considered as ecological functions. Some examples are: photosynthesis, nitrogen fixation, de-nitrifaction, carbon storage, decomposition, mineralization, soil aggregation, precipitation interception, or population regulation through, e.g., herbivory or carnivory, *inter alia*. In a more abstract sense, these can also be thought of as the parameters facilitating change in niche spaces, and therefore as the fundamental forces behind ecological structure. *Ecological function* is a useful conceptual tool for making evolutionary processes systematically coherent, as long as its

	implicit reductionism is sufficiently recognized: its terminology should not be confused with teleological interpretations of Darwinian biology.
Gene flow	The spatiotemporal exchange of genetic material between populations.
Heterozygosity (and *homozygosity*)	When the genes of an organism contain more than a single copy of all their material (haploid), and this structure is inheritable, one locus may contain different alleles, or gene-copies. A *homozygous* individual has identical alleles in the same locus, a *heterozygous* individual does not. Degrees of *heterozygosity* in a population can be considered analogously, and sometimes equally, to genetic diversity.
Interspecific indirect effects (IIGEs)	The effect of one species' genotype on another's phenotype through manipulation of the latter's environment. See Whitham et al. (2006) for examples and discussions.
Leaf symptom morphological species (or, *leaf morphospecies*, or *morphospecies*)	A species of leaf symptom morphology. In the context of this study, leaf morphospecies refers to species of differentiated symptoms of foliar exploitation, e.g. folds, galls, miner residues, cocoons, and varying types of herbivory. See Methods for a longer – but brief – explanation, and Appendix 7 for the full list.
Masting (or *mast fruiting*)	Every 2-10 years, throughout Asia, the sub-family Dipterocarpoidae Burnett, *inter alia*, will mass-produce fruits through synchronized flowering. These events are called "mast events" or "mast fruiting events" or similar things. In fact, many angiosperms (flowering trees) throughout the world behave like this. Often, weather events are considered causes. For the Asian dipterocarps (Dipterocarpoidae), many researchers agree that the El Niño-Southern Osccillation seems to be the primary cause for mast fruiting events (e.g. Curran et al. 1999; Curran & Leighton 2000).

Metabolics	The study of metabolic processes and their products. Can also be a collection of metabolic products, say as a variable in a model.
Neotropics	A eurocentric, but widely accepted, term for the tropical regions of Central and South America (*neo*="new"). Analogously, the tropical regions of Afroeurasia are frequently called the "old tropics", or sometimes the *paleotropics* (*paleo*="old").
Pedogenesis	The formation (*genesis*) of soil profiles (*pedon*).
Pollination syndrome	Since flowering plants depend on pollen vectors for successful reproduction, the vectors drive related flower trait evolution through natural selection. Large dipterocarp flowers do not exclude large pollinators, which forage across larger distances than smaller pollinators, increasing plant gene flow. This, in theory, homogenizes flower traits across populations and therefore leads to phenotypic convergence. Meaning, flower and pollinator sizes influence each others' evolution. The differentiation of the manifold flower trait phenotypes due to these kinds of interactions is aptly considered pollination syndrome.
Phytochemistry	The study of plant-related chemicals, or *phytochemicals*.
Phytosociology	The study of vegetative compositions; how they form, behave, and maintain their communities; the dynamics of collections of plants, or phytocoenoses. In forest trees, *phytosociology* often simply refers to canopy strata. This is the ubiquitous theme of this term in this thesis; how trees form canopies and interact with each other within them.
Plant Economic Spectrum (PES)	In order to produce conceptual structure in the interacting complexes of plant metabolism and ecology, the Plant Economic Spectrum (PES) provides a framework for interpreting plant behavior and biochemistry along the spectrum of acquisitive to conservative strategy; from fast to slow growth, and any kind of explicit or implicit ecological "trade-

	offs" relating to these strategies. See the landmark papers by Wright et al. (2004) and Reich (2014).
Pleiotropy (structured and unstructed)	Genetic expression is not linear, but complex. One gene does not necessarily code for a phenotype in one trait, but sometimes many. This is called *pleiotropy*. In the context of the Plant Economic Spectrum (PES), antagonistic *pleiotropy* realizes itself as trait trade-off (negative trait co-variance). See discussions in Roff & Fairbairn (2007) and Züst & Agrawal (2017).
Progeny and *provenance*	Where *progeny* identifies a line of descendants from a particular individual, *provenance* specifies its place of origin. *Provenance*, as a pragmatic proxy, is frequently used in forestry for streamlining adaptation in selecting tree *progeny* for specific site conditions.
Rarefaction	In community ecology, *rarefaction* is an analytical tool to compare community structure, say, between treatments or habitats, by normalizing sample sizes. If two communities were sampled with different effort (sample sizes), a fair comparison might require reducing the samples to equal sizes. This can be done, for instance, by bootstrapping. See Chao & Jost (2012) for some discussion on *rarefaction*.
Species diversity (*alpha*, *beta*, and *gamma*)	There are many different measures of different kinds of diversities. Commonly, and usefully, these are conceptualized as *alpha*, *beta*, and *gamma diversity*. *Alpha diversity* measures the diversity of species in a single site, say, a forest. *Beta diversity*, measures the similarity (or, more often, dissimilarity) of species compositions between two sites, say, two forests. And *gamma diversity* measures the total diversity of species of a larger area, say, a landscape. See Whittaker's (1972) landmark paper on these concepts, and also MacArthur's (1965) paper on within- and between-habitat diversity.

Specifics (*inter*-, *intra*-, and *con*-)	These terms are used to refer to certain species. *Con*- refers to a species in question (e.g. a specific dipterocarp species), *inter*- to groups between species (e.g. differences between dipterocarp species), and *intra*- to groups within species (e.g. to progeny of a certain dipterocarp species).
Strategy (ecological)	Westoby (1998) defines *strategy* as the means with which “a species sustains a population”. Because populations change through generations of individuals, their *strategies* are subjects of natural selection and are therefore able to adapt. Inidividuals might, similarly, strategize to maximize their fitness. But since these are temporally limited to the individuals’ life-span, they do not change due to selection, and are usually separatel considered *life history strategies*. See Reich (2014) for some discussion on ecological *strategies*.
Trait	A phenotypic property. See Reich (2014) for discussion on plant *traits*.
Xerophication (and *mesophication*)	Systematically inducing relatively xerophytic (dry environment with little water availability) conditions in an otherwise more humid ecosystem or landscape, transforming its foundational processes and driving the composition and dynamics of its species. Essentially the opposite of *mesophication*, which Nowacki & Abrams (2008) identify as, fundamentally, the loss of fire-related vegetative succession dynamics in North American forested landscapes following European settling. Latałowa et al. (2015) and Samojlik et al. (2022) also identify the loss of regional forest fires and fire-related human activities as very likely drivers of recent vegetative compositional shifts in the forests surrounding Białowieża, Poland.

Introduction

Background

Bornean dipterocarp forests, and some conservation issues

Dipterocarpaceae Blume (dipterocarps) is a pantropical family of flowering trees under the order Malvales Juss. ex Bercht. & J.Presl. The species of tropical Asia are all grouped into the subfamily of Dipterocarpoideae Burnett (dipterocarpoids) (IPNI 2024). During subfamily-synchronized masting – in dipterocarpoids, every 2-10 years –, dipterocarps bear distinct fruits whose sepals grow into wings, inducing gyration while falling (Greek: *di* = two, *pteron* = wing, *karpos* = fruit). For commerce, they constitute the most valuable native family of tree species for all of Asia (and possibly the world; see Curran et al. [2004] and Ghazoul [2016:211–248]), and are exploited industrially for utility on large scales. Dipterocarps typically dominate acrisol- and peat-rich and -associated lowland to sub-montane mixed forests (decreasingly from 400 to 1800 m a.s.l.) where they often, naturally, form the canopy and become giant emergent trees. Additionally, a large amount of, but not all, species of dipterocarps frequently form associations, in varying degrees of dominance, in ecologically adjacent systems: in ombrotrophic alluvial peat forests, arenic to podzolic lowland heath forests (*kerangas*), supratidal riparian fringes (Corner's [1940:42] *Saraca*-streams and *Neram*-rivers), periodically inundated semi-swamp forests (Symington [1943:xix] calls these "lopak forests"), and though the family is generally considered calciphobous, a few survive even on limestone rock. In some capacity, all these habitats occur on the island of Borneo, the world's richest region and radiative center of dipterocarps, with 13 genera and 269 species, of which 162 (60 percent) are considered endemic (Symington 1943; Curran et al. 1999; Ashton 2004; Ghazoul 2016:69–88; Ashton et al. 2021; Bartholomew et al. 2021). As a function of their spatial isolation, islands may host many more endemic vascular plant species than comparative mainland regions (Kier et al. 2009). And due to the Indo-Malayan archipelago islands' considerable areas, they become global hotspots for plant endemism and therefore unique extended life-systems (Murali et al. 2021; Schrader et al. 2024). Consequently, Borneo, and many other neighboring Sunda islands, are indispensable for biological conservation.

Plants function as essential foundations, both as substrate and facilitators, for complex trophic structures. And the plants of Borneo's dipterocarp forests, specifically, produce and host some of the most species-rich such structures in the world (Clarke & Kitching 1993; Kessler 1996; Schulte 1996; Momose et al. 1998; MacKinnon et al. 2013). Dipterocarps not only facilitate this complexity, but are themselves hosts for manifold interactions. Their infrequent supra-annual masting regulates populations of pollinating bees, beetles, thrips, flies, wasps, moths, and granivorous insects, birds, and mammals, which all either consume dipterocarp fruits or each other (Momose et al. 1998; Curran & Leighton 2000; Nakagawa et al. 2005; Wong et al. 2005). And during general flowering of intermasting periods, many generalist insects – e.g. lepidoptera larvae, orthoptera nymphs, and adult beetles and phasmids – feed on their flowers and leaves (Momose et al. 1998; Eichhorn et al. 2007; Junker et al. 2008; Chung et al. 2011). Besides directly spawning trophic complexity, dipterocarps also facilitate the growth of a host of climbers, stranglers, and epiphytes – e.g. lianas, bryophytes, lichens, figs, and ferns –, whose structures and leaf litter trappings provide utility for wefts of detritivores (Appanah et al. 1993; Ellwood et al. 2002; Harrison et al. 2003; Shahpuan et al. 2019; Pesiu et al. 2021; Thüs et al. 2021). Anthropogenic manipulation of the inter- and intraspecific composition of these plant populations induces significant change in their complex communities, potentially initiating localized extirpation (Symington 1943:xii–xxiii; Ashton et al. 2001; Boyle et al. 2021). Which, through the interaction of endemism, extreme heterogeneity, habitat fragmentation, and ecological degradation – all common on Borneo –, might escalate into extinction (Allouche et al. 2012; Cazzolla Gatti & Velichevskaya 2020; Bartholomew et al. 2021; Danylo et al. 2021; Colwell & Feeley 2025).

Given the relatively large species richness and radiative potential of Bornean dipterocarp forests, losses of these habitats through deforestation and ecological conversion have a disproportional potential for biological loss globally, both in localized unique density and transregional adaptive capacity. Alas, as a consequence of being foundational for their native ecology, an industrially highly valued forest resource, and inhabiting most of Borneo's most fertile soils, anthropogenic exploitation and land-use – specifically, conversion through forest management, and deforestation for mining and cultivation of crops like oil palm (*Elaeis* spp. Jacq.) and rubber trees (e.g. *Hevea brasiliensis* [Willd. ex A.Juss.] Müll.Arg.) –, have made many species of dipterocarps endangered and subsequently threatened their extremely diverse associated ecosystems (Symington 1943; Ashton 2004; Gaveau et al. 2014; Abood et al. 2015; Ashton et al. 2021; Bartholomew et al. 2021).

Climate and soil in dipterocarp evolutionary history

Recent findings propose elevation as a primary driver of genetic differentiation in tropical trees and shrubs, including dipterocarps (Axelsson et al. 2023; Middleby et al. preprint), placing the observed floristic divisions (speciations) of dipterocarp forests along both elevation and soil gradients (Symington 1943:vi–xxiii; Aiba & Kitayama 1999) in an evolutionary context. Some dipterocarps seem to have adapted to specific soil conditions with limited spatial distributions (Palmiotto et al. 2004; Baltzer et al. 2005; Itoh et al. 2012; Sukri et al. 2012); its diversity of soils, geographic barriers, and relatively stable perhumid climates of the Miocene and Pleistocene are considered to have been vital for the rich radiation throughout Southeast Asia. Following a Gondwanan emigration by the Indian plate, it seems as if fluctuations in climate, through contraction and expansion of rainforest habitat, drove both dipterocarpoid extinction and speciation in contemporary South Asia. Suggesting that their genetics are sensitive to climatic proxies (Ashton & Hall 2011; Ghazoul 2016; Ashton et al. 2021).

Equatorial species, having evolved in extreme heat and perhumid environments, importantly, seem to lack the option of poleward migration should future climates drive their habitats further into subhumid alternative states. Instead, their (potential) distribution shifts seem entirely limited to elevation. Implying likely further induced biological loss through inter- and intraspecific competition when communities migrate upslope, possibly causing biotic attrition (species loss without replacement) in what intact lowland dipterocarp forests are left (Pang et al. 2021; Colwell & Feeley 2025). And so, interactively, loss of lowland dipterocarp forests through anthropogenic means and climate change-induced competition along elevational gradients will likely continuously amplify the demand for genetic conservation of lowland species and upland restoration and management.

Some principles of dipterocarp forest restoration

The late-successional mixed evergreen rainforests dipterocarps dominate on Borneo tend to develop fully layered – complex – canopies, across families (Aiba & Kitayama 1999; Sist & Saridan 1999; Hector et al. 2011). Implicitly, post-logging recruitment is a considerable issue for silviculture, as consecutive exploitation easily may terminate late-successional stratification dynamics, leading to sustained ecological degradation (Symington 1943:xii–xiii; Appanah 1998; Sist & Saridan 1999; Ashton et al. 2001). And since all forests require a contextualized continuous succession of native tree species in order to retain their unique biology, the maintenance and imitation of natural canopy stratification has become the primary goal of dipterocarp silviculture. Regeneration of these forests are principally limited to natural means. Largely due to their inherent compositional complexity, a lack of streamlined breeding programs, and labor costs associated with artificial regeneration (Symington 1943; Appanah 1998; Ashton et al. 2001; Grady & Axelsson 2023; Axelsson et al. 2024)—which breeding programs, if fully developed, of course, might out-pace in revenue (e.g. Evans 1982; Grady & Axelsson 2023).

Across the tropics, uniform plantations, mostly of exotic species, have become the norm for industrial forest-related commodity pipelines (Evans 1982; Albrecht 1993; de Jong et al. 2021), leading to considerable contemporary forest conversion and associated biodiversity loss (Richardson & Rejmánek 2011; Wilcove et al.

2013; Gaveau et al. 2014; Phillips et al. 2017). Symington (1943:xx–xxi) notes that introduced semi-deciduous and subtropical species (e.g. *Eucalyptus* spp. L'Hér, *Pinus* spp. L., and *Oxytenanthera nigrociliata* Munro), which capitalize from novel disturbances (cultivation, grazing, cutting, drought, and fire) and induce some (drought and fire), prevent re-establishment of the native vegetation their introductions extirpated locally by forming complex compositions with dipterocarps and other late-successional native trees.

Not only do exotic invasive species chronically disturb natural canopy stratification, a collection of land-use methods have been identified as particularly detrimental for the conservation of dipterocarp forest succession—specifically when the vegetative dynamics of the understorey are disturbed. Intense cropping and understorey exploitation continuously interrupt tree recruitment, and logging operations exhaust the stock of reproductive mature trees while facilitating drought and fire-related disturbance severity by opening up the canopy and accumulating collateral residue as pyrogenic fuel. The establishment of the lower stratum of dipterocarps (and their natural associates) become disrupted in particular. As such, enrichment planting and supplementary liberation treatments are indispensable tools for effective restoration work (Woods 1989; Ashton et al. 2001; Banin et al. 2022; Axelsson et al. 2024).

Integrating native tree species into silvicultural practices sustaining foundational ecological processes could potentially restore prior and curb additional losses (Bremer & Farley 2010; Axelsson et al. 2022). And even though tropical lowland forests – in contrast to their boreal and temperate counterparts – may contain hundreds of native tree species (e.g. Schulte 1996; Sist & Saridan 1999), their benefit to associated biodiversity is not uniform; relatively small selections of tree species may – when contextually appropriate (Banin et al. 2022) – provide significantly larger restoration potential than random samples, befitting common logistical demands of both commercial and restoration practices (Axelsson et al. 2022). However, mapping out the necessity of safeguarding these species' genetic diversity, and therefore contribution to their extended phenotypes (Whitham et al. 2003, 2006), are important for maintaining ecological resilience, especially across extremely diverse landscapes (Axelsson et al. 2023) with potentially limited local adaptive capacities in light of current disruptive land-use and future climate changes (Tito de Morais et al. 2015; Grady & Axelsson 2023).

In the context of management, whether for restoration or commerce, all implicit assumptions of sufficient reproductive potential following local logging and regional habitat loss, and a sustained genetic diversity necessary for avoiding extinction vortices, need to be checked. Pipelines for development and deployment of seedlings, both for site adaptation and the conservation of genetic diversity, are paramount, yet vacant.

Relevance of seed-sourcing

Seed sourcing mechanisms for site-adaptivity are well developed and considered vital in the management of boreal and temperate forests (e.g. Matthews 1989; Savill 2019). These typically aim to maximize growth while avoiding losses due to stresses and disturbances. This is often framed as increasingly important throughout developing climate changes—for dipterocarps no less. Partly due to the predicted increase of both frequency and intensity – through interaction – of abiotic and biotic disturbances (Yusuf & Francisco 2009; Seidl et al. 2011; Bellard et al. 2012; Seidl & Rammer 2017), and partly due to dipterocarp extinctions correlating with global cooling beginning in the late Miocene lasting through the Pliocene (Ghazoul 2016:74–88; Ashton et al. 2021). And since many of the Bornean lowland dipterocarp forests have been – and are being – lost to silvicultural and agricultural conversion (Cazzolla Gatti & Velichevskaya 2020) without adequate genetic conservation, their unique lowland intraspecific genetic reservoirs become threatened, implicitly bereaving adaptation potential to future demands on restoration and land-use (Axelsson et al. 2023; Grady & Axelsson 2023).

Although variations in plant genetic traits have significant impacts on both growth and drought tolerance, this dimension of forestry is severely understudied for the native tree species of Southeast Asia. Implicitly suggesting that – in light of encroaching alternative states (Hapsari et al. 2022) – guidelines for seed-sourcing as criteria in site adaptation for forest management have considerable potential for restoring and maintaining the ecological functions of these forests (Axelsson et al. 2023; Grady & Axelsson 2023). Additionally, associated trophic effects should influence the extended phenotype of the entire system (Whitham et al. 2003, 2006; Axelsson et al. 2022). And in interaction, the system should influence the local adaptation of tree populations.

Theoretical framework

The plant economic spectrum

In the pursuit of maximizing fitness, plants may behave according to some set of empirically identifiable strategies. Though necessarily reductionistic, these strategies and their comparison offers a framework for causally understanding the drivers of trait evolution. Traits such as fast and thin or slow and dense wood growth (Wright et al. 2010), heavy investment into large and few or small and many flowers (Kettle et al. 2011), large and industrious or small and resilient leaves (Dudley 1996), costly and efficient or cheap but unreliable defenses (Mohanbabu et al. 2023). As suggested, these traits are usually conceptualized as continuous opposites, since the significance of their quantities depend on their relative association—fast and slow, thin and dense, few and many, large and small, reliable and not. Consequently, these strategies – as functions of natural selection – exclude their opposites, and are therefore conceptually considered trade-offs; directional trait evolution is exclusionary, but not necessarily due to physical limitation, e.g. resource allocation (Züst & Agrawal 2017), nor requiring linearity (Roff & Fairbairn 2007). Trade-offs may simply reflect gradients of fitness-maximizing trait combinations if their syntheses are, antagonistically, molecularly coupled, e.g. through pleiotropy (Roff & Fairbairn 2007; Züst & Agrawal 2017). The opposing typical strategies are those of: acquisition – through fast growth, resources may be seized efficiently – and conservation – by investing in costly defenses, any potential harm might be mitigated and minimized through resilience (Wright et al. 2004; Reich 2014; Züst & Agrawal 2017; Gorné et al. 2022).

Differentiation along these traits may even manifest within communities. Pioneer species quickly colonize disturbed microsites, now rich in available resources, but die sooner due to weak resilience-invesments (acquisition). Slow-growing shade-tolerant species, instead, survive beneath the canopy and rely on returns in the long run while minimizing short-term mortality (conservation) (Wright et al. 2010). Therefore, both strategies are functions of environmental selection; generally, rich resource availability promotes acquisitive traits, whereas continuous scarcity induces conservative traits in this plant economic spectrum (PES) (Wright et al. 2004; Reich 2014).

In seasonal, semi-open, savannas with fire and drought-related stress, conservative traits – i.e. thick leaves and low growth – develop in generalist woody plants with limited shelter. The same generalists, conversely, develop acquisitive traits – i.e. large specific leaf area (SLA, the ratio of leaf area to mass) and high contents of foliar nitrogen (N) and magnesium (Mg) – under deciduous canopies. Open-habitat-related species produce thicker bark and high foliar carbon (C)-contents, whereas forest-related species have evolved means to increase foliar contents of phosphorus (P), potassium (K), and calcium (Ca) (Maracahipes et al. 2018).

In perhumid environments, dipterocarp seedlings, within and between species, respond differently in height and basal area (BA) growth along elevational gradients, suggesting that their evolutionary responses, and thus ecological functioning, vary along climatic proxies like elevation and humidity (Axelsson et al. 2020, 2023). Additionally, dipterocarps, not only, differentiate along gradients of foliar chemistry (N, P, and K) and physical growth (SLA, wood density, and height growth), but their associated beetle communities respond to these traits (Axelsson et al. 2022). Hinting at realized extended phenotypes as functions of dipterocarp genetics; interdependent genotypic expression through vast interaction.

Extended phenotypes

Through the environment and itself, the genotype of any one organism produces a phenotype. This is the confined organism's genetic expression. If we simply extend the reasoning behind this mechanism into the trophic complexities of ecology, quickly a network of interspecific dependency on the communal genotypic dynamic emerges. Because the environment literally includes all organisms in close vicinity, which might influence the genotypic expression of any one individual of concern, the phenotype of all interacting organisms will depend on the others'. However, the relative influence on the environmental parameters regulating phenotypic expression in any one species of an ecosystem is not partitioned equally among its interdependent constituents. Some species have a larger impact on the environments surrounding them, others are or become the environment themselves almost entirely. This would depend on the environmental conditions and parameters influencing the expression of a specific genotype. Therefore, when the fitnesses of any two species are interdependent, their relative genotypes, through their expression, will influence the others'. We can imagine this relationship to be unidirectional if one does not influence the others' fitness, i.e. when their relationship is only unidirectionally dependent. Extend this idea to the entire ecosystem and the dimensionality of interspecific genetic influence across it must at least equal its species richness. But since any one relationship may be multidirectional and itself influence another, this space ought to be many times larger and much more complex. This extension – of the significance of one species', or organism's, genetic expression to another's – is the extended phenotype; heritability in community structure and thus their aggregate evolution (Whitham et al. 2003, 2006). These interspecific indirect genetic effects may describe the phenotype of a two-way relationship or an entire ecosystem, and any nested composition between them.

Simple phenotypic differentiation in natural hybrids of *Eucalyptus risdoni* Hook.f. and *E. amygdalina* Labill. produce gradients of overlap in communities of phytophagous insects typical of either conspecific parent, half of which only co-occur on the hybrids and some seem to specialize on. Consequently, both species abundance and richness maximizes on intermediate hybrids, producing an ecotonal response along genetic similarity (Whitham et al. 1994). A synthetic population of the same hybrids in a common garden, similarly, produced arthropod community gradients, with a corresponding chemotypic shift in defensive compounds—hinting at a causal link from plant genetics to community ecology through metabolics (Dungey et al. 2000). Similar cause-effect relationships have been hypothesized in avian community ecology (Bailey et al. 2006) and ecophysiology through phytochemistry (Dubiec et al. 2013)—as well as physical properties related to crown architecture (Martinsen & Whitham 1994; Bailey et al. 2004) and foliar thermal conductivity, light absorption, evapotranspiration, and affinity for decomposition (see hypotheses in Dubiec et al. 2013). When common starlings (*Sturnus vulgaris* L.) and blue tits (*Cyanistes caeruleus* L.), throughout courtship and paternal care, line their nests with non-randomly selected aromatic herbs rich in volatile secondary metabolites, nestling weight increases, their development improves, and probability of ectoparasitic infection may decrease if they, conspecifically, respond to secondary metabolic activity and their presence significantly influences nestling fitness (Mennerat et al. 2009; Dubiec et al. 2013; Gwinner et al. 2018).

Though the expression of extended phenotypes do not require chemical pathways across trophic levels as necessity. Even intraspecific genotypic variance, from allopatric progeny with inhibited local co-evolutionary history, may induce genetic drift and thus significantly alter the dynamics of associated communities. Exotic genotypes of the common reed (*Phragmites australis* [Cav.] Trin. ex Steud.) have been introduced to North American populations (Saltonstall 2002), which outcompete native progeny and reduce species richness in associated native systems (Benoit & Askins 1999). This cryptic invasion has been exacerbated through anthropogenic disturbances, facilitating exotic progeny dominance through expansion into degraded wetlands (Chambers et al. 1999). Thus, the expression of extended phenotypes are additionally influenced by environmental factors, which themselves could be subjected to change as PES-traits may fundamentally alter chemical cycling (Treseder & Vitousek 2001). Progeny selection of foundation species, therefore, possesses the potential to upheave the mechanisms sustaining their trophic wefts (Whitham et al. 2003, 2006).

Research scope

Principal synthesis

Elevational gradients can work as proxies for climatic variation and therefore environmental selection on differentiated populations of dipterocarps, a foundational pantropical family of trees. Such gradients should be able to predict adaptation to non-sexual selection pressures. By sourcing seedlings from wild mother trees and growing them in common gardens, effects from environmental selection can be inferred across progeny.

In heterogeneous landscapes, such as the tropical rainforests of Borneo, the phenotypic variation and genetic adaptive capacity both within and between species may be large (Axelsson et al. 2023), whose responses still require principal elucidation (Grady & Axelsson 2023). In light of future climatic demands on land-use systems, unfolding the weft of these mechanisms will be crucial for maintaining the potential for genetic adaptation at both local and regional levels—for the sake of ecological functioning in trees, but probably extended phenotypes as well (Whitham et al. 2003, 2006; Axelsson et al. 2022).

Hypotheses

1. Dipterocarps differentiate intraspecifically along gradients of functional plant trait-expression, and
2. environmental stress, induced by elevation and soil aridity, influences this differentiation.
3. Dipterocarp progeny express different extended foliar phenotypic structure,
4. which follow gradients of genetic similarity, proxied by mother tree elevation and soil, and
5. are influenced by functional plant traits.

Methods

Design and data

Common garden history and floristics

Following masting in 2019, throughout 3 weeks, fruits were collected from wild trees of *Parashorea tomentella* (Symington) Meijer (frequently referred to as PT), *Shorea argentifolia* Symington (SA), *Shorea fallax* Meijer (SF), and *Shorea johorensis* Foxw. (SJ) around southeastern Sabah, Malaysia (*Figure 1*). These were propagated, *ex situ,* in shaded germination beds filled with sawdust and regularly watered. All beds included half-sibs from all progeny to control for unwanted spatial effects (block design). All germinated seedlings were potted in 1 liter plastic bags with 1:1 mixtures of mineral soil and compost, and received 2 g of Agroblen™ fertilizer twice: one month and one year post germination (for more information on operation procedures, see Axelsson et al. [2024]). In May of 2022, about 2.7 years after seed collection, following 3 consecutive days of rain, the half-sib seedlings were planted in pre-dug holes in a common garden (4°37'40" N, 117°19'20" E) about 16.4 ha in size (*Figure 2*).

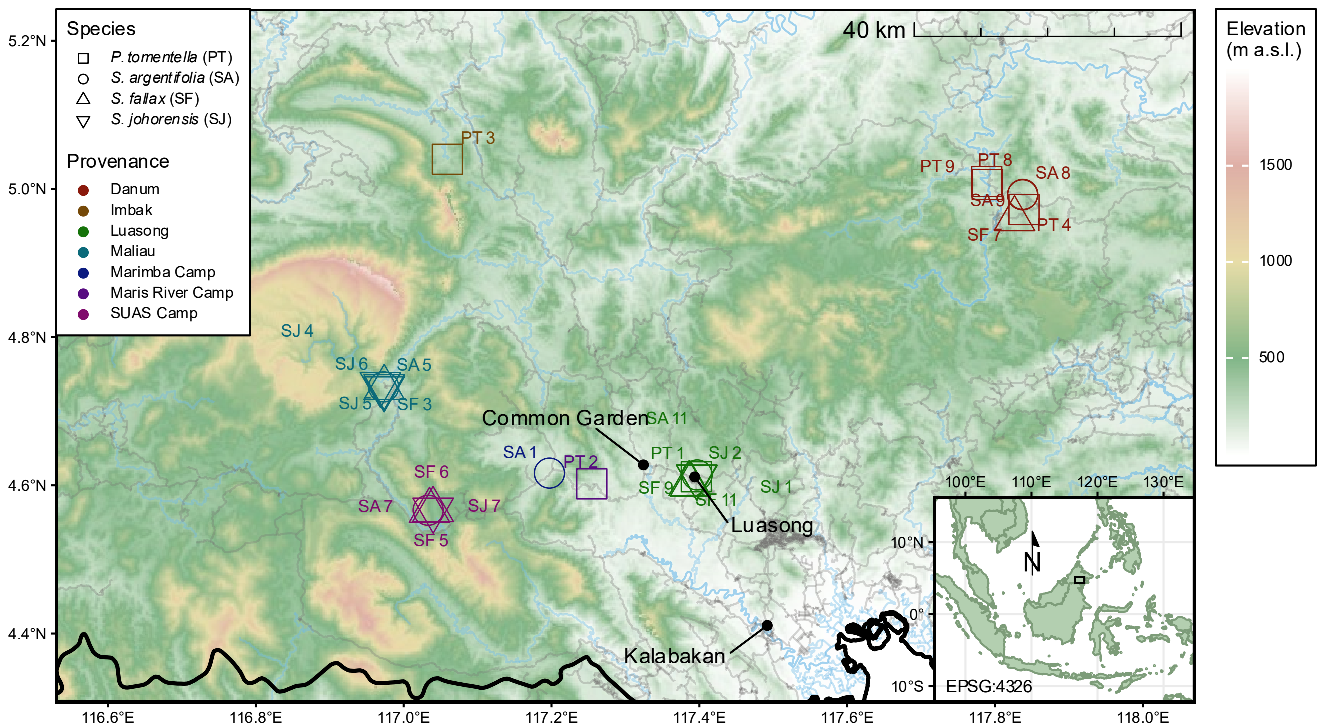


Figure 1. Distribution of mother trees in south-eastern Sabah. Tree species as shapes and provenances as their colors (see *Table 1*) over land elevation (mean elevation in 7.5 arc-second rasters, USGS 2010). Roads (grey lines) and rivers (blue lines) from OpenStreetMap contributors (n.d.), available under the Open Database License (ODbL).

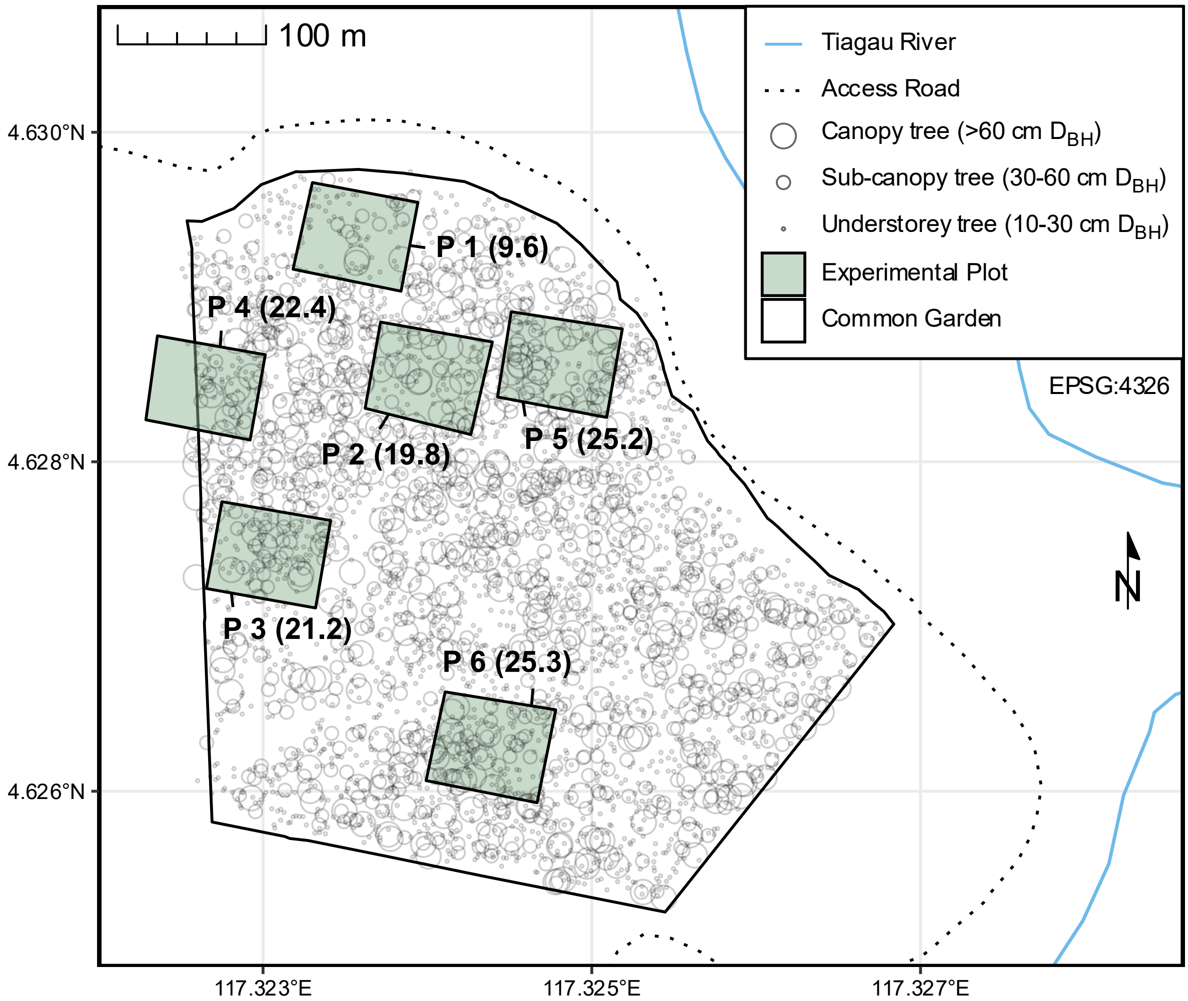


Figure 2. Common garden layout with experimental plots (and their estimated basal areas [$\widehat{BA}$] in m²/ha). Spatial configuration of trees of different D_{BH}-classes as circles in sizes corresponding to their size categories. Since P 4 was partly outside the common garden, its $\widehat{BA}$ only reflects 58 percent of its total area.

The common garden borders the Tiagau river and an access road to the north and east, and is located approximately 80 km northwest of Tawau, around 130 m a.s.l (USGS 2010). The site's interpolated local mean annual precipitation (MAP) and temperature (MAT) between 1970 and 2000 was 2282 mm and 26.2 °C, and consistently aseasonal (Fick & Hijmans 2017). Beck et al. 's (2018) modified Köppen-Geiger model classifies the regional climate as tropical rainforest (Af) under present-day (1980 to 2016) conditions. The soil of the common garden is dominated by orthic acrisols with associations of dystric cambisols of sand- and mudstone on very high hills with slopes commonly >25° (Key 39 in Acres et al. [1974]).

The stand is a logged forest once regenerated with mahogany (*Swietenia* sp.

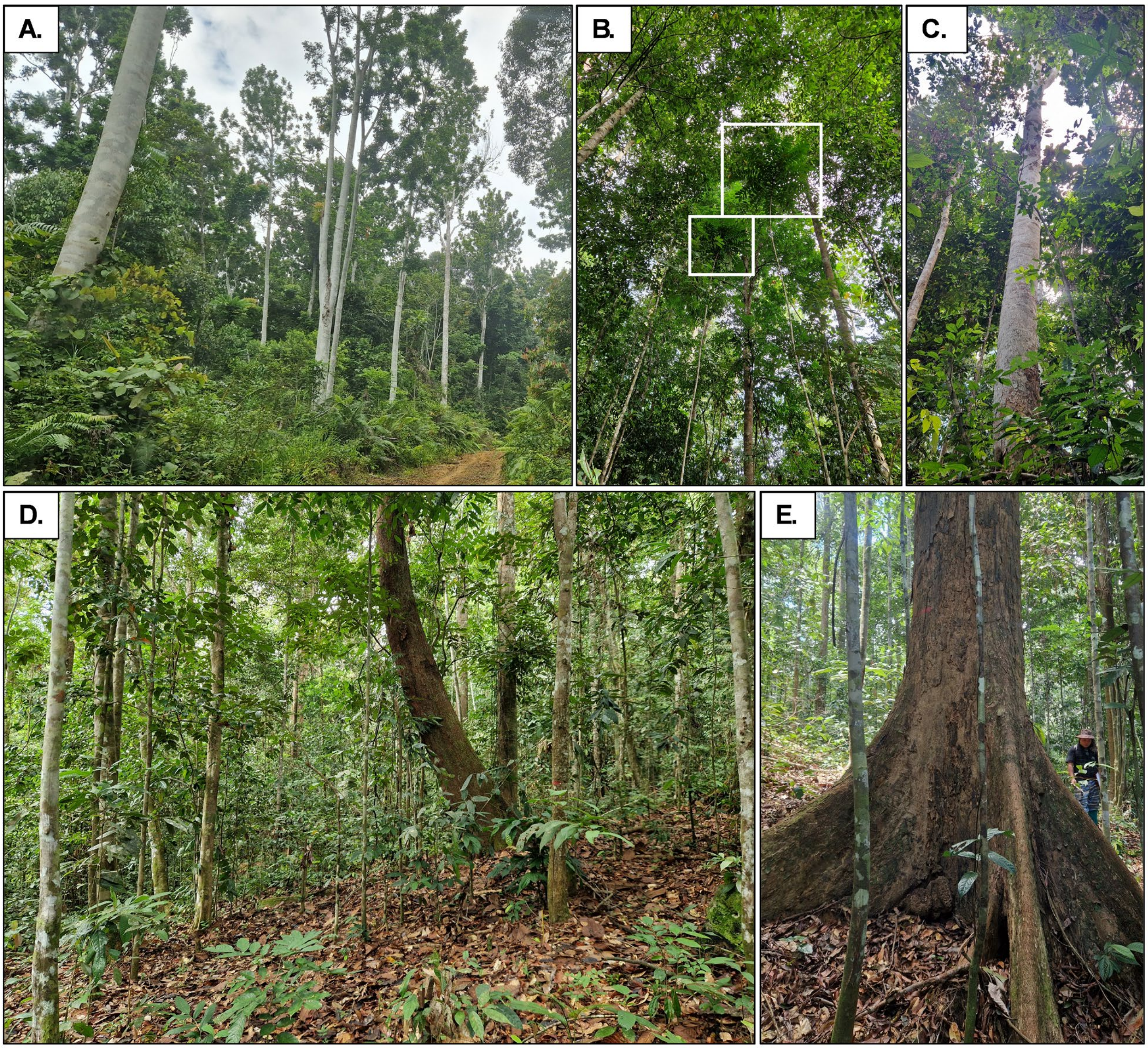


Figure 3. Prevalent forest strata in and surrounding the common garden: **A.** introduced mahogany (*Swietenia* sp. Jacq.) in the canopy outside the common garden along the access road, **B.** naturally regenerated mahogany in the understorey of plot P 3 (crowns inside white boxes), **C.** mahogany in the canopy of plot P 4, **D.** variation in stem diameters in plot P 5, and **E.** larger stem buttresses of a dying canopy tree in plot P 4 (see plots in *Figure 2*).

Jacq.). Both degrees and methods of the loggings are unknown, but the mahoganies were planted on this site in the early 1900s for seed production (personal communication with Albert Lojingi). They still make up a significant part of the canopy, with considerable recruitment both inside and outside the common garden (*Figure 3*)—the genus is considered invasive in comparable Philippine dipterocarp forests for these, and related, reasons (Baguinon et al. 2003). At some time the plantation was likely abandoned, and has now become part of the Sow-A-Seed project (Axelsson et al. 2024). The purpose of this experimental setup is to investigate the restorative effects of enrichment planting by native late-successional tree species, i.e. dipterocarps, in degraded forests, and any variations in this respect due to genetic heritage.

Along the mahoganies, dipterocarps frequent the canopy, with associations of Euphorbiaceae Juss., Fagaceae Dumort., Lauraceae Juss., Moraceae Gaudich., and Malvaceae Juss. Emergent trees are noticeably lacking; most likely due to the previous loggings. The canopy is only partially closed, with sporadic significant openings. Beneath, the structure is complex, with a dynamic composition of grasses, ferns, vines, palms, lianas, gingers, and seedlings (*Figure 4*), whose

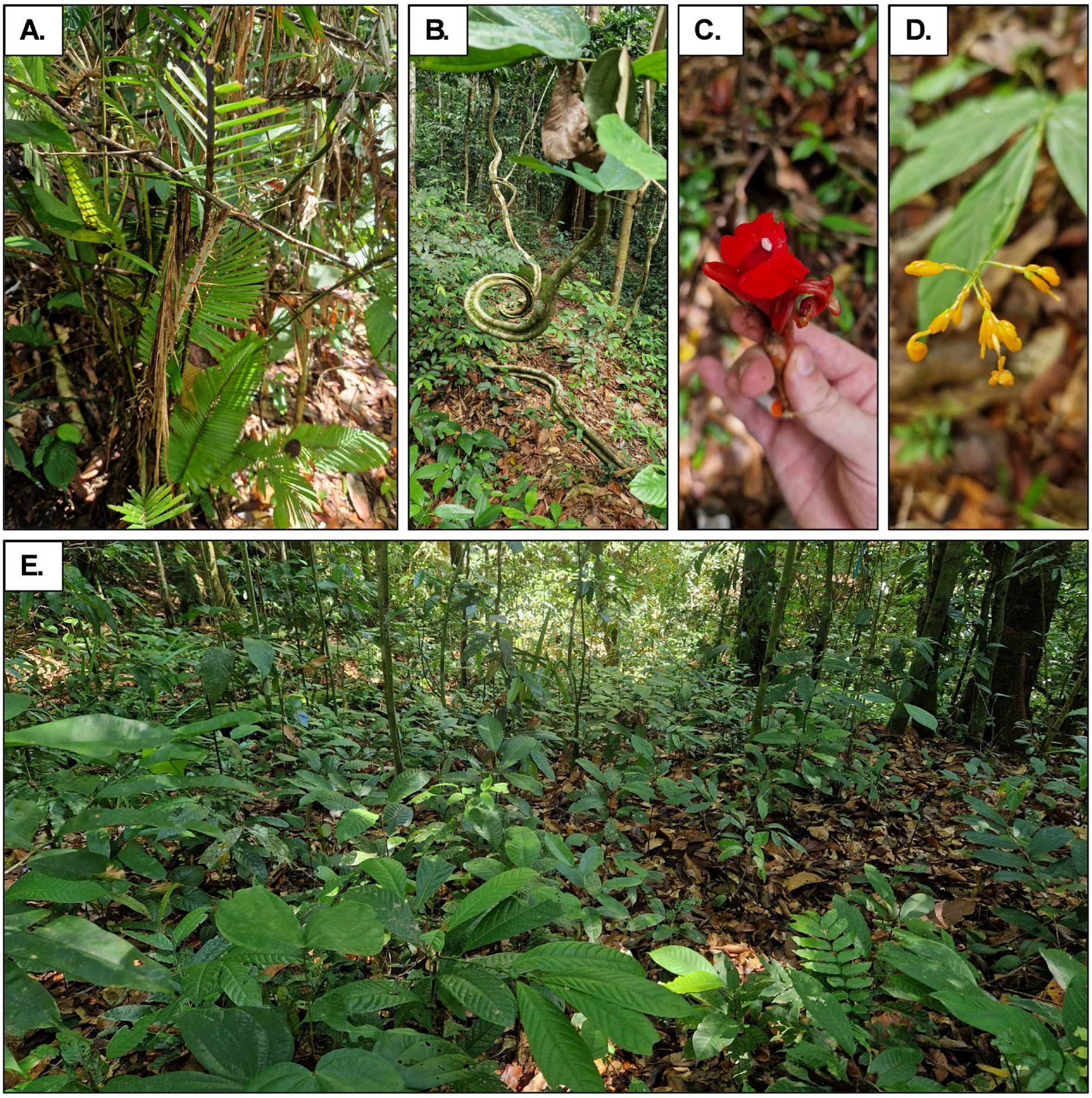


Figure 4. Some understorey floral diversity of the common garden: **A.** a small rattan palm (Arecaceae Bercht. & J.Presl), **B.** lianas hanging between canopy trees, **C.** and **D.**

common gingers (Zingiberaceae Martinow), and **E.** a blanket of dipterocarp recruitment and other vegetation.

configurations seem to largely depend on the spatial distribution of openings of varying degrees; grasses, vines, and ferns occur mainly in larger openings, and where the canopy has closed, moisture and slope seem to determine whether the field layer is dominated by ferns, palms, or seedlings with ginger admixtures.

Experimental design

In order to homogenize effects due to the spatial distribution of the planting in the common garden, five individuals of each progeny of all species were randomized along 2 m wide parallel rows in each plot (including progeny of other species not investigated here: *Parashorea malaanonan* [Blanco] Merr., *Shorea leptoderma* Meijer, *Shorea pauciflora* King, *Shorea smithiana* Symington, and an unknown *Shorea* Roxb. Ex C.F.Gaertn. sp.). The center of the rows were separated by 4 m, and the trees along the rows by 3 m. The median (even sample size) plot size was 0.445 ha, the maximum 0.473 ha, and the minimum 0.419 ha. Each row was continuously cleared from competing vegetation to support plant establishment (effectively, continuous liberation treatments) (see *Figure 5*).

Within the common garden, the plots were distributed to maximize differences in canopy closure to produce a gradient between them. And in parallel with

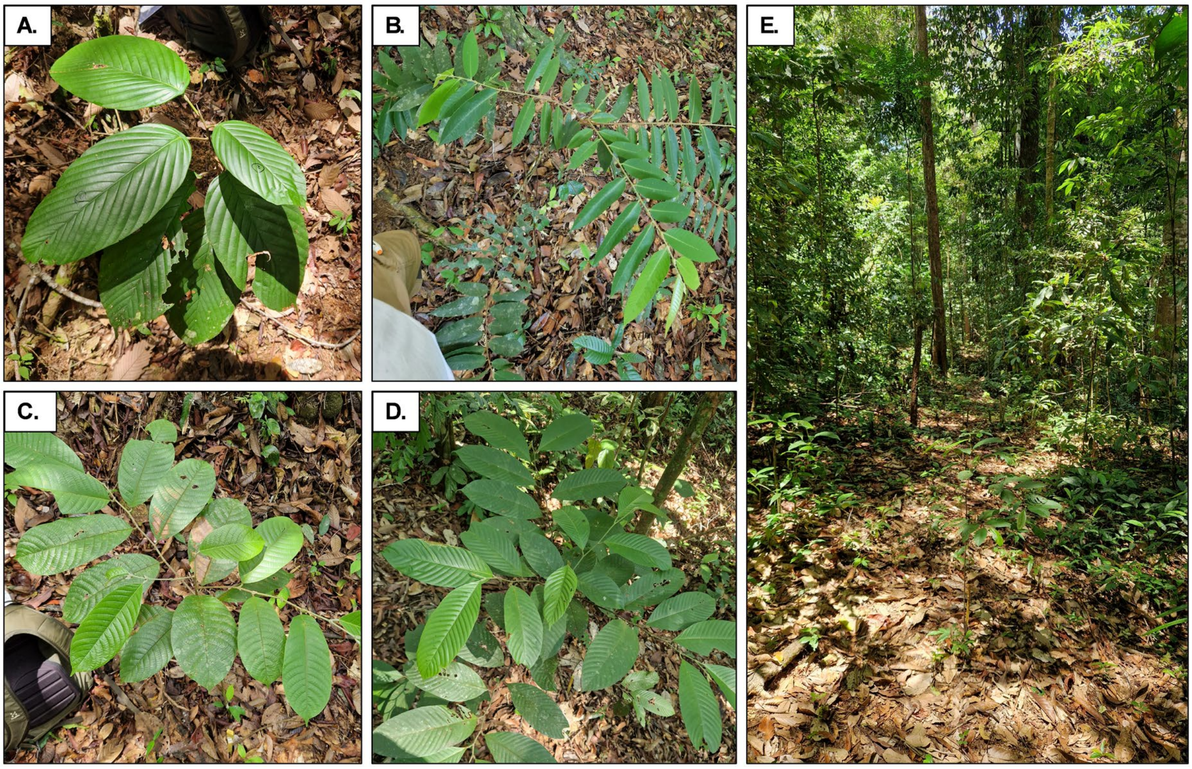


Figure 5. Planted trees in the common garden, plot P 5: **A.** *Parashorea tomentella* (Symington) Meijer, progeny PT 3, **B.** *Shorea argentifolia* Symington, progeny SA 8, **C.** *S. fallax* Meijer, progeny SF 7, and **D.** *S. johorensis* Foxw., progeny SJ 1. And **E.** a planting line in plot P 2.

planting, trees inside the common garden, with diameters at breast height (D_{BH}, 130 cm above germination point) >10 cm, were geopositioned and put in one of three groups: 10-30 cm, 30-60 cm, or >60 cm. From this, a rough BA estimate ($\widehat{\mathrm{BA}}$) can function as a proxy for within-plot vegetative competition. Since D_{BH}-density distributions are typically right-tailed in these canopy systems (Aiba & Kitayama 1999; Sist & Saridan 1999; Hector et al. 2011), the average D_{BH} of all groups would likely not be the arithmetic mean of the groups' constraints. However, this would likely still yield an underestimate, since the largest D_{BH} class is an open category without upper limit and many trees obviously had a D_{BH} >60 cm. Whether an overestimate or not, though, this provides a standardized quantity of within-plot overstorey competition. This $\widehat{\mathrm{BA}}$ should not be misconstrued as a basal area estimate. Between the plots, $\widehat{\mathrm{BA}}$ ranged from 9.6 to 25.3 m^2/ha (*Figure 2*), and the overall $\widehat{\mathrm{BA}}$ of the common garden was 18.0 m^2/ha (see Appendix 1 for D_{BH}-densities).

Tree species and progeny selection

Tree species were chosen to maximize differences in mother tree elevation as a proxy for climatic influences on intraspecific phenotypic variation. Adherence to or deviation from the PES can then be inferred intraspecifically. And by comparing fit responses to mother tree elevation and soil, some light may be shed on their relative influences on dipterocarp evolution. See progeny statistics and provenance in *Table 1*.

Inventory and sampling

Height, D_{base} (diameter 10 cm above germination point), and understorey light illumination (as Clark & Clark's [1992] crown illumination index, CII) were measured and estimated for every tree. Since height and D_{base} were measured for all trees 1.4 years prior, relative growth rates (RGR) in these traits were also estimated as

$$\mathrm{RGR} = \frac{\ln(M_{0+t}/M_0)}{t},$$

where M_{0+t} and M_0 are either height or D_{base} from this, 0+t, or the last, 0, inventory, where t is the positive difference in time (around 1.4 years here). RGR standardizes for initial differences in M, and is fit for comparison to coefficients from linear regressions of ln(M) (see Turnbull et al. 2012).

Three leaves were chosen as representative for the mean leaf area per tree and then photographed against a decimeter reference. Leaf areas were estimated

Table 1. Species-wise progeny and their mother trees' height, diameter at breast height (D_{BH}), soil key (from Acres et al. [1974], see *Table 2*), and elevation. And Pearson correlation between mother tree elevation (r_{Elev}) and climatic variables (MAT=mean annual surface temperature, ΔT=difference between maximum and minimum annual temperatures, SRAD=mean annual surface daily incident solar radiation, MAP=mean annual precipitation) from Fick & Hijmans (2017). Sorted alphabetically by Progeny ID.

Species[a]	r_{Elev}[b]	Progeny ID	Mother height (m)	Mother D_{BH} (cm)	Mother elevation (m a.s.l.)	Mother soil key[c]	Provenance	Latitude (N)	Longitude (E)
Parashorea tomentella (Symington) Meijer		PT 1	41	80.5	135	12	Luasong	4°36'56.4834"	117°23'45.312"
	MAT=-0.94	PT 2	40	52.3	201	48	Maris River Camp	4°36'21.996"	117°15'16.4154"
	ΔT=-0.32	PT 3	42	112.0	256	48	Imbak	5°2'38.9034"	117°3'32.6874"
	SRAD=-0.35	PT 4	32	78.0	301	40	Danum	4°58'34.5"	117°50'20.6874"
	MAP=0.14	PT 8	48	89.0	160	26	Danum	5°0'51.1914"	117°47'19.104"
		PT 9	34	70.0	188	26	Danum	5°0'35.9994"	117°47'21.696"
Shorea argentifolia Symington		SA 1	47	115.5	150	30	Marimba Camp	4°37'14.3034"	117°11'49.992"
	MAT=-0.96	SA 5	31	56.2	233	10	Maliau	4°44'13.092"	116°58'22.692"
	ΔT=-0.61	SA 7	46	66.8	476	48	SUAS Camp	4°34'13.692"	117°1'59.304"
	SRAD=-0.71	SA 8	58	105.0	293	40	Danum	4°59'48.1914"	117°50'14.7114"
	MAP=0.21	SA 9	38	82.0	266	40	Danum	4°59'46.284"	117°50'13.488"
		SA 11	40	45.0	129	40	Luasong	4°37'5.304"	117°23'49.2"

[a] From IPNI (2024).

[b] Climate variables from Fick & Hijmans (2017).

[c] Keys from Acres et al. (1974).

Table 1. (continued)

Species[a]	r_{Elev}[b]	Progeny ID	Mother height (m)	Mother DBH (cm)	Mother elevation (m a.s.l.)	Mother soil key[c]	Provenance	Latitude (N)	Longitude (E)
Shorea fallax Meijer		SF 3	40	35.5	219	39	Maliau	4°44'8.808"	116°58'25.2114"
	MAT=-0.98	SF 5	40	65.7	464	48	SUAS Camp	4°34'11.7834"	117°2'5.892"
	ΔT=-0.79	SF 6	37	40.9	422	48	SUAS Camp	4°34'16.212"	117°2'23.0994"
	SRAD=-0.55	SF 7	25	49.0	283	40	Danum	4°57'48.708"	117°49'34.6074"
	MAP=0.72	SF 9	48	67.5	141	30	Luasong	4°36'22.392"	117°23'10.6074"
		SF 11	43	70.7	129	30	Luasong	4°36'18.8994"	117°23'16.908"
Shorea johorensis Foxw.		SJ 1	34	42.0	129	12	Luasong	4°36'55.584"	117°23'48.5874"
	MAT=-0.99	SJ 2	42	63.9	129	12	Luasong	4°36'56.9874"	117°23'46.284"
	ΔT=-0.66	SJ 4	29	57.0	221	10	Maliau	4°44'15.6114"	116°58'25.284"
	SRAD=-0.26	SJ 5	39	87.3	229	39	Maliau	4°44'4.992"	116°58'24.8874"
	MAP=0.90	SJ 6	44	77.5	226	10	Maliau	4°44'26.0874"	116°58'6.9954"
		SJ 7	40	57.2	423	48	SUAS Camp	4°34'15.888"	117°2'23.784"

[a] From IPNI (2024).

[b] Climate variables from Fick & Hijmans (2017).

[c] Keys from Acres et al. (1974).

Table 2. Acres et al.'s (1974) soil keys and their definitions (from *Table 1*). Sorted by Soil rank.

SoilKey	Ong & Kleine's (1995) ranks	Soil rank[a]	Soil category[b]	Terrain	Soil material	Soil groups
10	-	1	Good (1)	Valley floors	Alluvium	Gleyic and dystric cambisols (dystric and eutric fluvisols, gleyic and orthic acrisols)
26	-	2	Good (1)	Low hills and minor valley floors, slopes 0-15°	Mudstone and sandstone	Gleyic, ferric, and orthic acrisols (gleyic, ferric, chromic, and orthic luvisols)
12	-	3	Good (1)	Terraces	Alluvium	Orthic, ferric, and gleyic acrisols (gleyic podzols)
40	good	4	Intermediate (2)	Very high hills, slopes 15-25°	Mudstone and sandstone (misc. rocks)	Orthic acrisols (dystric cambisols)
30	-	5	Intermediate (2)	Moderate hills, slopes >25°	Mudstone and sandstone	Orthic acrisols (dystric cambisols)
39	good	6	Intermediate (2)	Very high hills, slopes >25°	Sandstone and mudstone	Orthic acrisols (dystric cambisols)
48	poor	7	Poor (3)	Mountain cuestas	Sandstone and mudstone	Orthic acrisols (dystric cambisols gleyic podzols, humic Gleysols, lithosols)

[a] From most (1) to least (7) fertile, inferred from Driessen (2001).

[b] With ordinal ranking for modeling. Inferred from Ong & Kleine's (1995) ranks, Soil rank, and Acres et al.'s (1974) definitions.

manually from these photos in *Digimizer* version 6.4.4 (MedCalc Software Ltd 2025). Due to photographic distortion, at times, the reference scale had to be adjusted manually. When leaf abundance was low (<10), all leaves were photographed and their overall mean was considered the mean leaf area instead. Total leaf area (TLA) was then estimated as the product of the mean leaf area and leaf abundance. Additionally, three of the most developed and vital leaves were photographed and sampled for weighing for SLA and phytochemical analyses. For the purpose of appropriately estimating SLA, heavily mined translucent leaf tissues were excluded from total leaf area.

Prior to sampling, foliar chlorophyll content was measured with an *Apogee Instruments, Inc.* MC-100 Chlorophyll Meter. After sampling, all leaves were oven-dried at 70 °C and weighed with an *OHAUS Instruments Co., Ltd.* Pioneer PA4102 Precision Balance until their repetitions converged (between 6-24 hours, depending on time between sampling and weighing). This was assumed to approximately equal their constant mass (but also investigated in Appendix 2).

Subsequently, for elementary contents, per sample, approximately 100 mg of ground leaf material was oven-dried at 105 °C overnight. The samples were then digested using a sulfuric acid-hydrogen peroxide method adapted from Allen (1989). The digestate was diluted to 50 mL using reverse osmosis-deionised water. N absorbance was estimated with salicylate green at 655 nm and P with molybdate blue at 880 nm with a *Shimadzu* UV2600i. And K with a *Spectro* Arcos FHM22 through ICP-OES (Anderson & Ingram 1993).

All georeferencing, raster analysis, and vectorization was done in *QGIS* (2024) version 3.34.12-Prizren.

Leaf symptom morphological species inventory

Leaf symptom morphological species (hereafter, leaf morphospecies or simply morphospecies) were inventoried for the purpose of investigating extended foliar community phenotypes. Any symptoms of differentiable foliar substrate use were considered their own species; organisms (e.g. insects) were not identified and counted, but their associated structures. Consequently, it was and is not possible to determine whether two leaf morphospecies were causes of one or more species of organisms, or even by two individuals of the same species of organism at different life stages. In order to minimize any bias from this taxonomic discrepancy, only small differences (e.g. leaf fold widths) were considered insufficient for differentiation. Identification, instead, required noticeably naive guidance (e.g. leaf fold location: leaf edge, tip, or center, etc.). As such, leaf morphospecies abuse the frequent interspecific phagy in herbivorous insects (Schoonhoven et al. 2005:6–13) to proxy associated communities of foliar exploiters; invertebrates and fungi—almost all symptoms were determined to very likely be effects of invertebrate exploitation and the others clearly fungal (having fruiting bodies and hyphae). The aptness of similar parataxonomic methods is unclear (e.g. Barratt et al. 2003; Abadie et al. 2008). However, in biogeographic environments where new plant species are discovered daily (Raven et al. 2020), few alternatives are more reasonable (echoing Modica et al. 2014).

A list of leaf morphospecies was continuously built throughout inventory (final list in Appendix 7, *Table 9*). Leaf morphospecies were counted as leaves per tree; one leaf may host many morphospecies, and so could be counted many times, but only once per morphospecies. Every leaf on every planted dipterocarp was inventoried for morphospecies to standardize sampling effort (Roswell et al. 2021). Leaf morphospecies on petioles were included, and if one was found on the stem, it was counted once. Through coverage-based species rarefaction and cumulative inventory efficiency, the compositions of the first two plots were determined to likely be comparatively insufficient, and were subsequently treated as trial runs to be revised *ad-hoc*. Secondary inventories of these plots (P 1 and P 4, see *Figure 2*) significantly shifted the *Chao*-space centroid locations of the leaf morphospecies communities (PERMANOVA$_{P1}$: $\widehat{F}_{1,\,77}$=7.82, $\widehat{p}$<0.01; PERMDISP$_{P1}$: $\widehat{F}_{1,\,77}$=2.21, $\widehat{p}$=0.15; PERMANOVA$_{P4}$: $\widehat{F}_{1,\,94}$=3.89, $\widehat{p}$<0.01; PERMDISP$_{P4}$: $\widehat{F}_{1,\,94}$=2.41, $\widehat{p}$=0.12; 9999 permutations each) and improved coverage convergence with non-trial runs of the other plots (see Appendix 3). Thus both validating the list and minimizing bias from sampling effort (Roswell et al. 2021).

Analysis

Phenotypic response

Progenic differentiation in both seedling trait expression and extended phenotype structure was modeled with analysis of variance (ANOVA); this is how hypotheses 1 and 3 were tested.

Axelsson et al. (2023) found linear relationships between seedling heights and basal areas to elevational gradients. And Axelsson et al.'s (2022) multivariate analyses produced significant linear relationships between dipterocarp traits and beetle diversity. Congruently, for testing hypothesis 2, seedling trait expression was modelled using Generalized Linear Models (GLMs); mother tree elevation and soil quality proxying genetic heritage, and CII and $\widehat{\mathrm{BA}}$ environmental influence. In compliment, Random Forest (RF) models can hierarchically determine which variable has the largest influence on the response. This is done by bootstrapping decision trees (therefore "Random Forests") and through sequential permutation determining which variable produces the largest gain in prediction error (Breiman 2001).

Since community responses along genetic gradients are expected to be non-linear (Whitham et al. 1994; Dungey et al. 2000; Allouche et al. 2012), Generalized Additive Models (GAMs) were used to estimate them non-parametrically. These are essentially GLMs which sum multiple basis functions inside penalized coefficient-smooths, therefore “additive models” (Hastie & Tibshirani 1986; Wood 2006). GAMs complicate inference somewhat, but allow for similar responses as Dungey et al.’s (2000), and therefore testing of hypothesis 4.

Seedling trait-foliar community dependency

Distance-Based Redundancy Analysis (db-RDA) is a constrained ordination method that treats matrices as responses to any matrices of predictors. Its ordinations are considered “constrained” because they do not maximize variance along the response axes, but by the set of predictors. Thus, these predictors constrain our ordination distribution. This, effectively, allows for investigating correlations between two matrices of grouped variables, e.g. leaf morphospecies abundances and seedling traits, and therefore testing of hypothesis 5 (Legendre & Anderson 1999; McArdle & Anderson 2001; Legendre & Legendre 2012b).

First, morphospecies abundance dissimilarities are decomposed through Principal Coordinate Analysis (PCoA) into principal coordinates (PCos). Second, PCo means are estimated through multiple linear regression with dipterocarp seedling traits as predictors. A matrix is constructed from the fitted PCos, whose ordination thus is constrained by the trait predictors through their linear fit—a multiple linear regression model is, effectively, a set of linear combinations on a single response variable. We treat the estimated PCos as pseudo-communities. Third, eigenvalues for the estimated PCos (explained constrained variance) and the modelled residuals (explained unconstrained variance) are decomposed through PCoA—again. We are not limited to Euclidean distances, but may use any dissimilarity matrix (therefore “Distance-Based” RDA). The total variance explained per constrained principal coordinate of the db-RDA is therefore the product of its individual explained variance and the explained constrained variance, adjusted for redundancy in constraining predictors (i.e. constrained-R^2_{adj} [c-R^2_{adj}]) (van den Wollenberg 1977; McArdle & Anderson 2001; Legendre et al. 2011).

Redundancy in the predictor matrix was identified through singular value decomposition (SVD) and collinearity with variance inflation factors (VIFs) (Legendre & Legendre 2012a). And finally, Lingoes’ (1971) method (Legendre & Anderson 1999) was used to correct for negative eigenvalues. All db-RDA was done with *vegan::dbrda(distance = “chao”, add = “lingoes”)* (Oksanen et al. 2025).

All $p<0.05$ considered significant. All statistical analyses were done with *R* version 4.4.3 (R Core Team 2025) in *RStudio* version 2024.12.1+563 (Posit Software 2025).

Alpha diversity

Hill (1973) provides a unifying notation for indices of alpha diversity as Whittaker (1972) formulates it conceptually: the density of species in niche hyperspaces. Hill diversity (D_q) is a function of the tunable parameter q, and is defined as

$$D_q = \left(\sum_{i=1}^{S} p_i{}^q\right)^{1/(1-q)},$$

where

$$D_1 = \lim_{q \to 1} D_q = e^{\left(-\sum_{i=1}^{S} p_i \ln p_i\right)}.$$

Here, p is the relative abundance of species i of all S observed species (the observed species richness). When q=0, Hill diversity (D_q) is equivalent to species richness (S or D_0). When q=1, it is the exponential of Shannon's (1948) H' (Hill-Shannon, D_1). And when q=2, it is the inverse of Simpson's (1949) λ (Hill-Simpson, D_2). Although, of course, any value of q may be chosen, even fractions (Hsieh et al. 2016). Hill diversity essentially estimates species equivalents, or the effective number of species with identical relative abundance, as a function of insensitivity to rare species (q).

Contrary to H' and λ, Hill diversity always (independently of q) satisfies MacArthur's (1965) expected doubling property: given two disjoint communities of equal species diversity K, their pooled diversity must equal $2K$. And since sensitivity to relative abundance scales with q, the synthesis of S, H', and λ under the framework of D_q makes their quantities comparable, and therefore the regulation of community diversity, with respect to rarity, amenable for analysis (Hill 1973; Hsieh et al. 2016; Roswell et al. 2021).

All Hill diversity calculation was done with *vegan::specnumber()*, *exp(vegan::diversity(index = "shannon"))*, and *vegan::diversity(index = "invsimpson")* (Oksanen et al. 2025), and coverage-based rarefaction, estimation, and extrapolation with *iNEXT::iNEXT(q = c(0, 1, 2), nboot = 200, conf = 0.95)* (Hsieh et al. 2024).

Beta diversity

Similarity indices help us estimate what Whittaker (1972) considers beta diversity: community overlap in habitat hyperspace. Effectively a spatial extension of niche hyperspace, which is analogous to treating community compositions as species in alpha diversity. This can be done in many ways, but most common quantitative approaches either considers similarity as relative distances between combinations of variables (e.g. Bray & Curtis 1957) or the proportional overlap in composition (e.g. Jaccard 1912; Chao et al. 2005). Since the indices weigh the variables differently in their compositional space, meta-properties of the data (i.e.

methodological constraints and analytical end) usually determine which index is the most appropriate for the hypothesis in question. Therefore, if the purpose of the use of these indices is to produce theoretically consistent matrices of similarity between observations, it is essential to find the index most appropriate for the ecological variables of interest (Magurran 1988). And lastly, when we are more interested in how the communities of two groups diverge, rather than converge, it is both intuitive and mathematically more appropriate to consider dissimilarity, rather than similarity, for analysis.

Chao et al.'s (2005) index (here, *Chao*) expands Jaccard's (1912) (J_{clas} in Chao et al. [2005]) from shared occurrence frequency into estimating pairwise abundance dissimilarity between observations in multivariate space. This is done by treating species discovery as a function of their relative abundances and comparing overlap in multivariate compositions at the individual level. This index is defined as

$$Chao = 1 - \frac{U \times V}{U + V - U \times V},$$

where U and V are estimates for the relative abundances of individuals belonging to the same species, and are defined as

$$U = \frac{C_j}{N_j} + \frac{(N_k - 1)}{N_k} \times \frac{a_1}{2a_2} \times \frac{I_j}{N_j}$$

and

$$V = \frac{C_k}{N_k} + \frac{(N_j - 1)}{N_j} \times \frac{a_1}{2a_2} \times \frac{I_k}{N_k}.$$

Here, C is individual abundance of shared species on sites j and k, N is total individual abundance (or, sample size) on sites j and k, a_1 is singleton abundance, a_2 is doubleton abundance, and I is the individual abundance of species at one site (j or k) with a corresponding singleton at the other. As such, when both sites approach absolute relative homogeneity ($U \rightarrow 1$ and $V \rightarrow 1$), the dissimilarity (*Chao*) approaches 0. Conversely, as compositions get richer in species, the relative abundance of individual overlap decreases ($U \rightarrow 0$ and $V \rightarrow 0$), and so *Chao* approaches 1.

As sampling converges with maximum coverage, doubletons become more abundant than singletons, and their ratio ($a_1/2a_2$) is minimized, punishing *Chao*. At the same time, I varies with coverage, since the probability of individuals sharing conspecifics depends on sample size (N). And so the I/N-ratio is the frequency of individuals with corresponding conspecific singletons, which leverages rare species by punishing *Chao* as inequity in individual overlap increases (large differences between individual- and singleton-rich sites). These ratios weigh U and V by their sample coverage, and since the relative abundances of similar individuals are treated separately for sample groups (Chao et al. 2005), *Chao* also accounts for differences in sample sizes. Conclusively, *Chao* is an appropriate measure of dissimilarity between ecological communities, but relies on the assumption of abundance data of individuals, and so is often not an appropriate index for dissimilarity in other domains, e.g. in phenotypic space with large range differences between dimensions (Chao et al. 2005).

All *Chao* matrices were calculated with *vegan::vegdist(method="chao")* (Oksanen et al. 2025).

Results

Some notes on inventory

In total, 720 trees were inventoried. Due to low leaf abundance, 28 percent of *P. tomentella* individuals' leaves were not sampled for SLA or phytochemical contents. Consequently, the lower end of total leaf area was not captured in this species, and so the phytochemical responses are less likely to produce noteworthy effects. Nevertheless, sample sizes were always ≥76 (see trait summary in Appendix 6, *Table 5*) and there was no noteworthy data-loss in the other species.

Overall, 82 identified leaf morphospecies were determined taxonomically comparable and therefore useful for analysis. Among these, 7946 were counted on 35210 leaves (see list in Appendix 7, *Table 9*). All interspecifically rarefied Hill diversities (D_0, D_1, and D_2) converged at ≥0.99 sample coverage in all four dipterocarp species (see Appendix 6, *Table 6*).

Seedling performance and traits

Univariate progenic differentiation

Progeny means varied significantly in multiple traits, but not in all species. Meaning hypothesis 1 was partly supported. In height RGR, there was significant variation between progeny of *S. argentifolia* ($F_{5, 91}$=3.21, p=0.01). There was no significant variation in D_{base} RGR between progeny of any species. Mean $\log_{10}$(TLA) was only significantly different between progeny of *P. tomentella* ($F_{5, 96}$=2.91, p=0.02). And there was significant variation in mean SLA between progeny of *S. argentifolia* ($F_{5, 88}$=4.62, p<0.01). Neither mean total foliar N or P contents differed significantly within any species. However, mean foliar chlorophyll content varied significantly between progeny of *S. argentifolia* ($F_{5, 91}$=5.29, p<0.01), and mean total foliar K between progeny of *S. argentifolia* ($F_{5, 91}$=2.59, p=0.03) and *S. fallax* ($F_{5, 92}$=6.54, p<0.01). Modeled with two-way ANOVA, with controls for plot-allocation. Residuals approximately Gaussian and homoscedastic (see Appendix 4, *Figure 17*).

Modeling intraspecific trait response, and model comparison

Mother tree elevation (Elevation) and CII only co-varied marginally—in all four dipterocarp species (r_{PT}=-0.04, r_{SA}=-0.21, r_{SF}=-0.11, r_{SJ}=-0.10). CII and $\widehat{BA}$ also, generally, did not co-vary considerably (r_{PT}=-0.05, r_{SA}=4.7×10^{-3}, r_{SF}=-0.42, r_{SJ}=-0.13). Mother tree elevation and soil quality (Soil) co-varied strongly however (r_{PT}=0.65, r_{SA}=0.65, r_{SF}=0.91, r_{SJ}=0.88; two-way ANOVA with species control: $F_{1, 432}$=38.57, p<0.01, residuals approximately Gaussian and homoscedastic [not

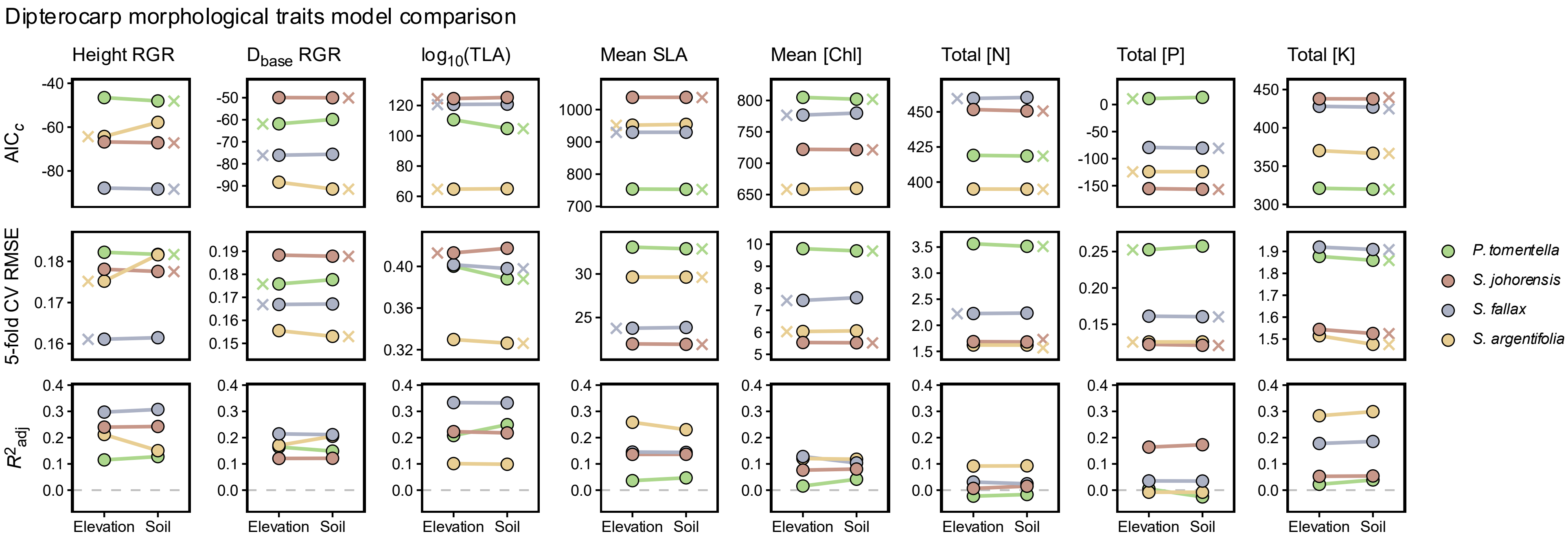


Figure 6. Model fit statistics (AIC_c, 5-fold cross-validated RMSE, and R^2_{adj}) for comparison of influence from mother tree elevation (Elevation) and soil quality (Soil) on height RGR, D_{base} RGR, log_{10}(total leaf area), mean specific leaf area (SLA), mean foliar chlorophyll (Chl) content, and total foliar N, P, and K contents. Total leaf area logged to fit model assumptions (residuals were right-tailed). Colored crosses (×) indicate species-wise AIC_c- and 5-fold cross-validated RMSE-favor. Convergence in mean RMSEs were decently consistent across models with 25 epochs (see Appendix 4, *Figure* 18).

shown, but skewness=-0.07 and kurtosis=-0.53]), and so their partial effects on trait expression could not be separated confidently by regressing responses on both. Instead, their trait-wise influences had to be investigated by model comparison (Akaike 1974; Kohavi 1995; Burnham & Anderson 2004).

Since linear interactions can confound additive relationships, full models with three main effects (genetic, CII, and $\widehat{\mathrm{BA}}$) and one two-way interaction (genetic×CII) – simulating phenotypic expression ($\mathrm{P} = \mathrm{G} \times \mathrm{E}$) with a within-plot control for vegetative competition ($\widehat{\mathrm{BA}}$) –, were compared to reduced models with only main effects. The genetic effect was fitted as either Elevation or Soil. The best fitting trait-wise models were then compared within species.

AIC_c favored the Elevation and Soil models 12 and 20 times each, respectively, with some variation between species and most traits (*Figure 6*). Soil was always the favored model for total foliar K content.

RMSE distributions were estimated with 5-fold cross-validation and differences ($\Delta RMSE=RMSE_{Elev}-RMSE_{Soil}$) compared. ΔRMSE favored the Elevation model 11 times and Soil 21 times. There was some variation between species, but no overwhelming support for either Elevation or Soil model (*Figure 6*). As from AIC_c, there was overwhelming support for the Soil model when predicting total foliar K. Elevation and Soil model selection varied a lot in the other traits (*Figure 6*). However, relative loss of RMSE between the favored and unfavored models ($\delta RMSE=\Delta RMSE/\max[RMSE_{Elev}, RMSE_{Soil}]$) was always small (all $\delta RMSE \leq 0.04$).

Total foliar K responses consistently favored the Soil model, though relative RMSE loss was always small (all $\delta RMSE \leq 0.03$). Both models' mean RMSEs converged decently at 25 epochs (see Appendix 4, *Figure 18*). Model favor in both AIC_c and ΔRMSE was interspecifically consistent in D_{base} RGR and total foliar P content (though all $\delta RMSE \leq 0.02$). No other clear inter- or intraspecific patterns were observed in Elevation contra Soil dominance on trait expression.

Intraspecific trait response to genetics

Trait response varied, not only, between genetic predictors (Elevation or Soil), but dipterocarp species. Hypothesis 2 was therefore supported; in some capacity, mother tree elevation and/or soil quality influenced trait expression in all four species. This expression was not always simple however.

In *S. argentifolia*, height RGR clearly responded to Elevation but not Soil, and D_{base} RGR produced an equivalent response to Soil and not Elevation. In other cases, such as for mean foliar chlorophyll content in *S. fallax* or total foliar P and K contents in *S. johorensis* and *S. argentifolia*, respectively, it was not possible to determine primacy in Elevation or Soil. Both because both modeled responses were significant (*Figure 7*) and model selection was not entirely convincing ($\delta RMSE_{Chl|SF}=0.02$, $\delta RMSE_{P|SJ}=0.01$, $\delta RMSE_{K|SA}=0.03$)—it rarely was. This might be a condition of how Soil was quantified (ordinal scale) and the magnitude of modeled noise (though total explained variance was not unreasonably small; $R^2_{\text{adj [Chl|SF]}}$=0.13, $R^2_{\text{adj [P|SJ]}}$=0.16, $R^2_{\text{adj [K|SA]}}$=0.28; see *Figure 6*). Nevertheless, separating causally intersected effects might be futile if said intersection is, either, large or necessary for expression (trade-off theory necessarily requires causal trait-interdependency). As such, these statistics often point towards influence, and rarely to dominance.

Five times ANOVA failed to predict genetic effects the linear models were able to identify ($\log_{10}$[TLA] in *S. johorensis* and *S. fallax*, D_{base} RGR in *S. argentifolia*, mean foliar chlorophyll in *S. fallax*, and total foliar P in *S. johorensis*). Meaning, in these cases, even though hypothesis 1 could not be supported, hypothesis 2 was. These discrepancies must be caused by some underlying responses, since the linear modeling effectively decomposes what ANOVA confounds. Except in the case of *S. fallax*' mean foliar chlorophyll, AIC_c always favored the inclusion of antagonistic interaction terms (*Figure 7*). These environmental influences effectively normalize the genetic differentiation, hiding responses as the progenic means are homogenized. Not only might these responses be overlooked in simpler models, but these and similar latent genetic influences imply likely differentiation as the seedlings mature and progenic environmental susceptibility compounds with time.

The significant, but antagonistic, effects on *S. argentifolia*'s height RGR by Elevation (partial-R^2=0.04, β=1.7×10^{-3}, SE=8.2×10^{-4}, t_{97}=2.11, p=0.04) and the Elevation×CII interaction (partial-R^2=0.06, β=-1.4×10^{-3}, SE=5.6×10^{-4}, t_{97}=-2.50, p=0.01) were approximately equal in magnitude (10000 non-parametric bootstrap replicates: $\overline{|\beta_{\text{Elev}}| - |\beta_{\text{Elev×CII}}|}$=3.3×10^{-4}, SE=2.9×10^{-4}, $\hat{p}$=0.26). Response in D_{base} RGR followed a similar pattern in the Soil model: significant increase from Soil (partial-R^2=0.04, β=0.35, SE=0.17, t_{97}=2.08, p=0.04), but decrease from Soil×CII (partial-R^2=0.05, β=-0.24, SE=0.11, t_{97}=-2.21, p=0.03). And, again, the magnitudes were roughly equal (10000 non-parametric bootstrap replicates: $\overline{|\beta_{\text{Soil}}| - |\beta_{\text{Soil×CII}}|}$=2.2×10^{-4}, SE=2.1×10^{-4}, $\hat{p}$=0.51).

S. fallax had a similar response in height RGR: both Soil (partial-R^2=0.03, β=0.22, SE=0.12, t_{108}=1.82, p=0.07) and the Soil×CII interaction (partial-R^2=0.02, β=-0.13, SE=0.08, t_{108}=-1.66, p=0.099) were almost significantly positive and negative, respectively. And the antagonistic magnitudes between Soil and the interaction were only close-to-significant (10000 non-parametric bootstrap replicates: $\overline{|\beta_{\text{Soil}}| - |\beta_{\text{Soil×CII}}|}$=0.08, SE=0.05, $\hat{p}$=0.08). Its $\log_{10}$(TLA) also, similarly, increased significantly with Soil (partial-R^2=0.04, β=0.63, SE=0.29, t_{108}=2.14, p=0.04) but decreased through the Soil×CII interaction (partial-R^2=0.04, β=-43, SE=0.19, t_{108}=-2.26, p=0.03). Which were, again, of only close-to-significantly different magnitudes (10000 non-parametric bootstrap replicates: $\overline{|\beta_{\text{Soil}}| - |\beta_{\text{Soil×CII}}|}$=0.20, SE=0.11, $\hat{p}$=0.06).

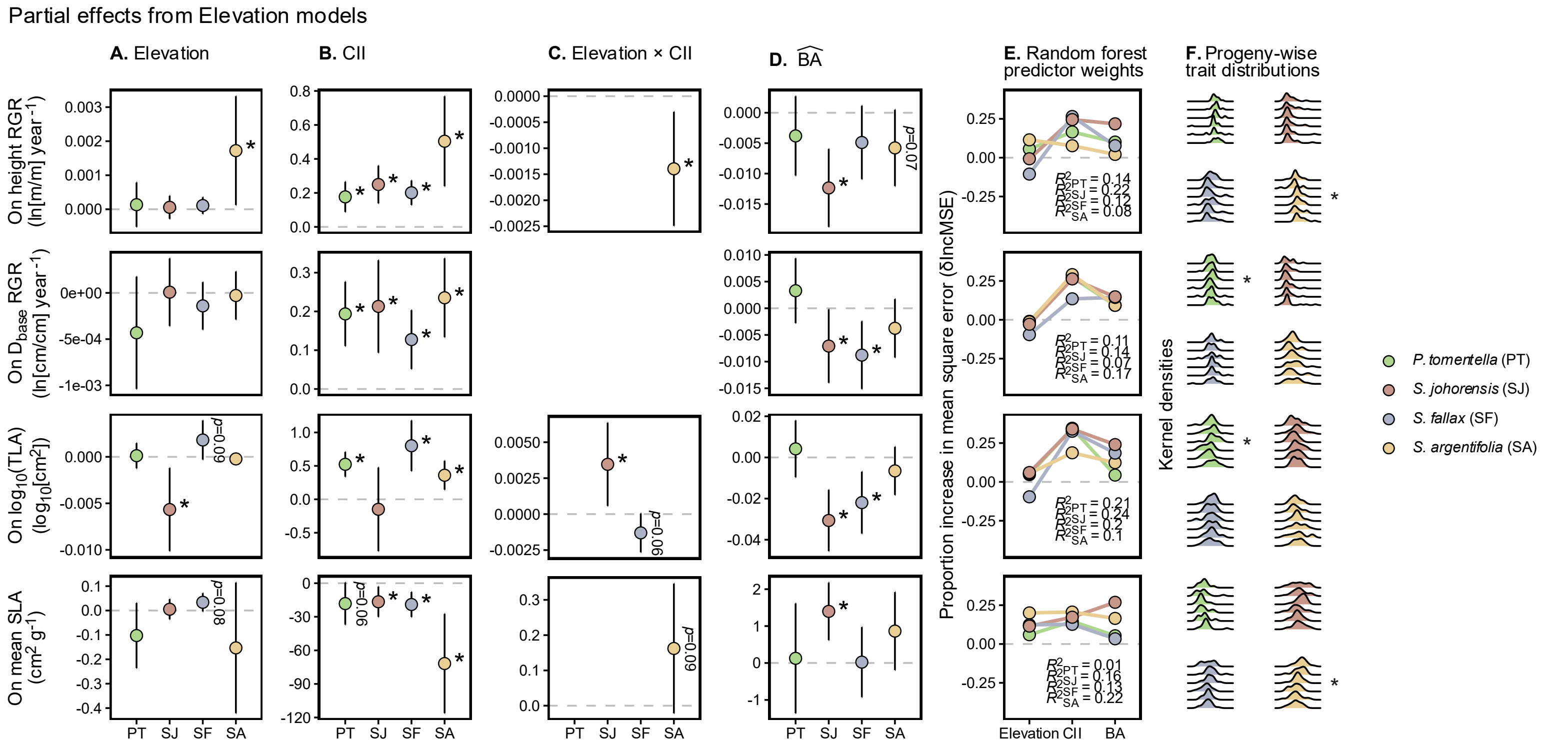


Figure 7. Partial effects on dipterocarp seedling height and D_{base} RGR, log_{10}(total leaf area), mean specific leaf area (SLA), mean foliar chlorophyll (Chl) content, and total foliar N, P, and K contents. Coefficients with 95 percent confidence intervals for **A.** genetic predictors (either mother tree elevation [Elevation] or soil quality [Soil, ordinally from fertile to poor]), **B.** seedling-wise canopy illumination index (CII), **C.** their interaction, and **D.** plot-wise estimated basal area ($\widehat{BA}$), with stars (∗) indicating significant (p<0.05) effects. With **E.** random forest predictor weights (δIncMSE) and their species-wise pseudo-R^2 (as R^2). Forests with 10000 trees, with 999 permutations each. And **F.** trait distributions, with stars (∗) indicating significantly different means between progeny when controlling for plot-allocation (two-way ANOVA). With progeny sorted, top to bottom, from lowest to highest Elevation or Soil. $76 \leq n_{PT} \leq 108$, all $n_{SJ}=115$, $101 \leq n_{SF} \leq 113$, $99 \leq n_{SA} \leq 102$. All responses modeled with Generalized Linear Models (GLMs) with identity links. Residuals approximately Gaussian and homoscedastic (see Appendix 4; *Figure* 19, *Figure* 20, *Figure* 21, and *Figure* 22).

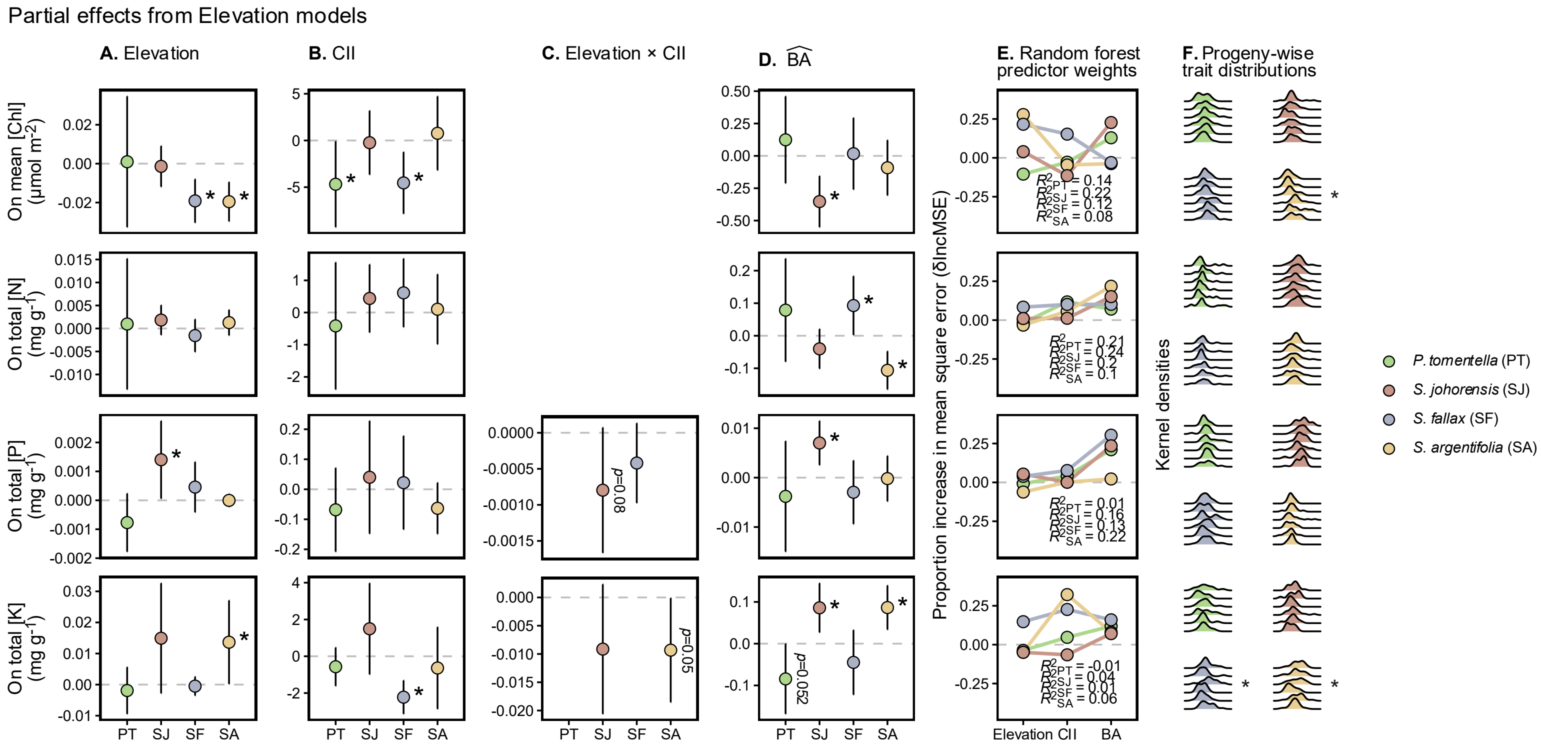
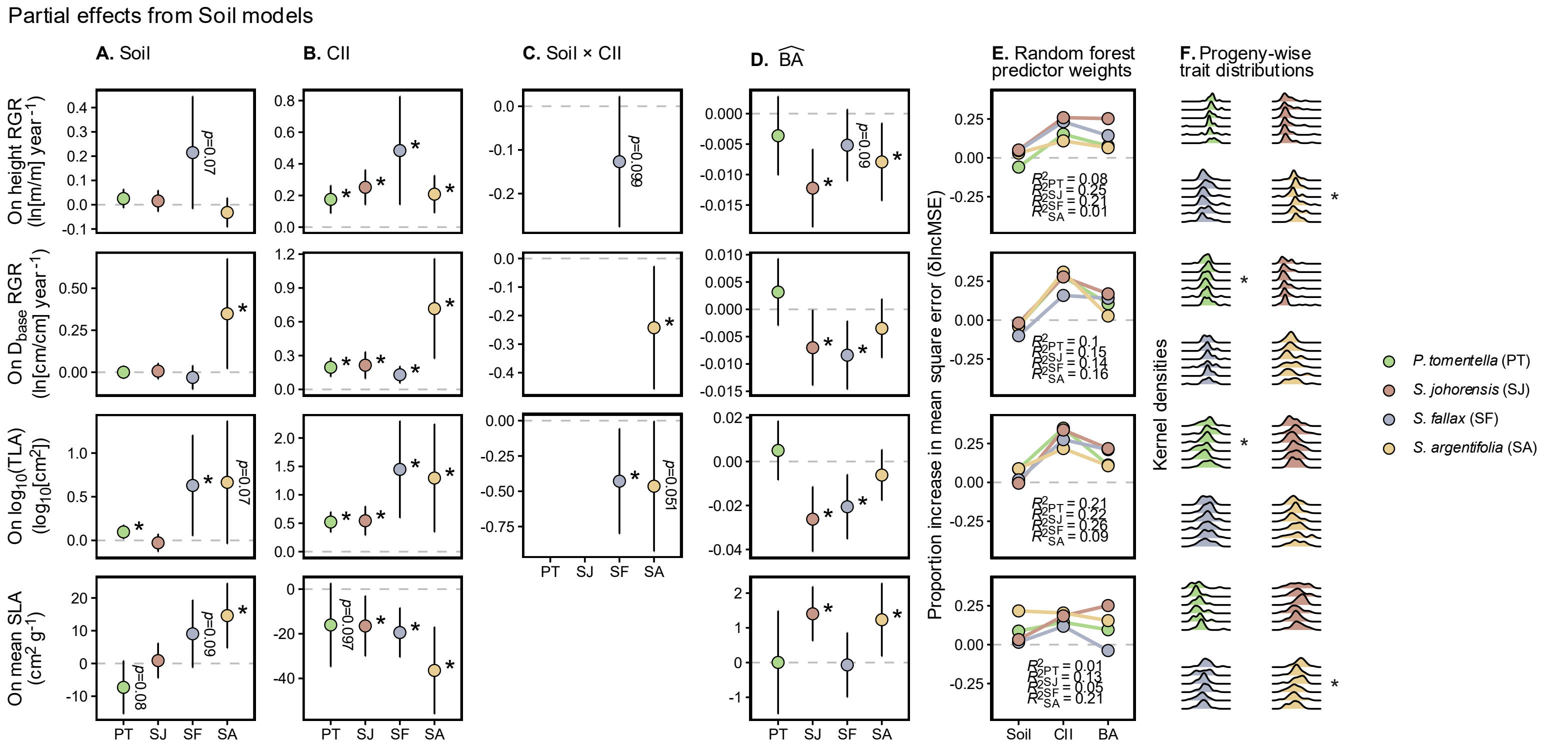


Figure 7. (continued)



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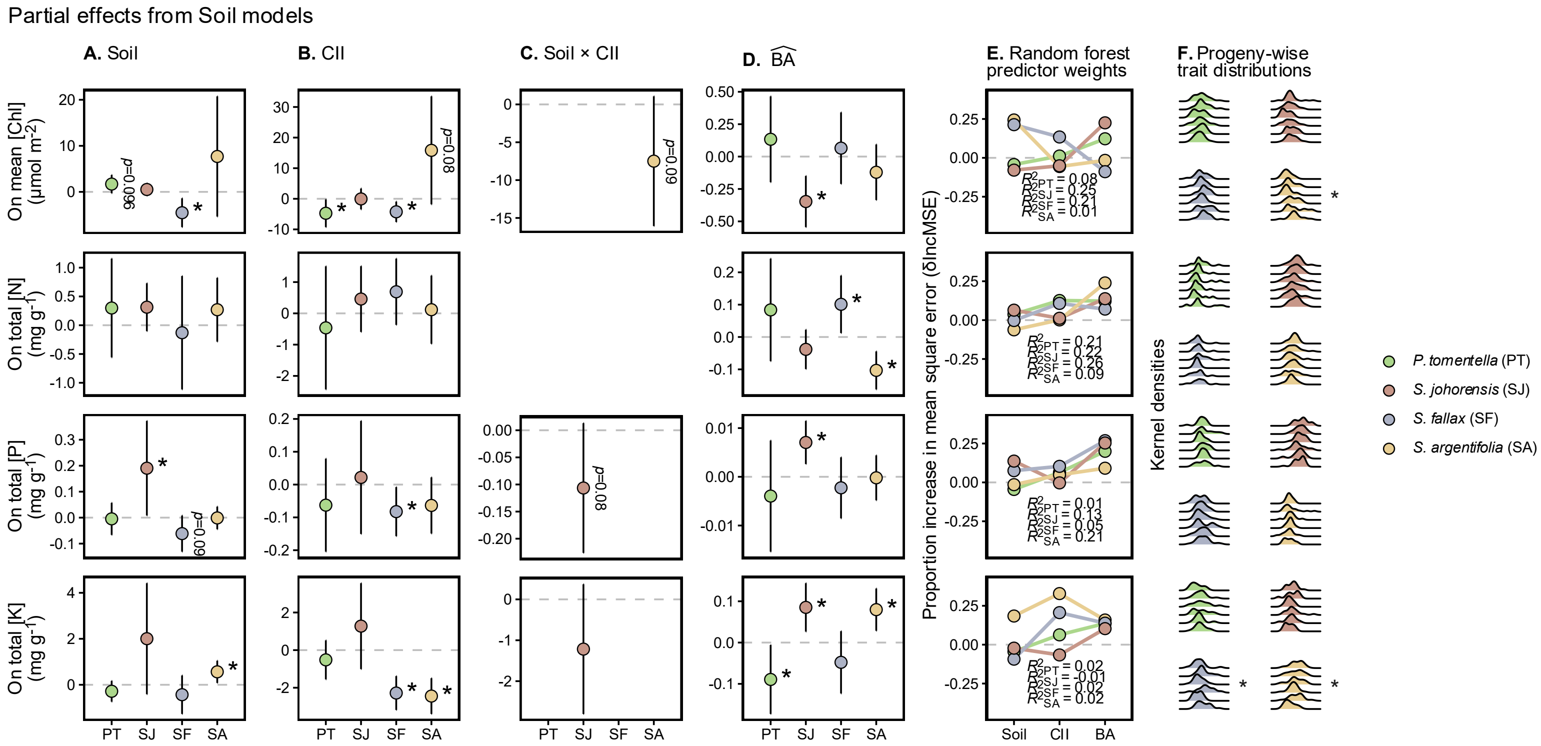

Figure 7. (continued)

Intraspecific trait response to environment

While the genetic effects on trait expression – both main and interactions –, varied a lot, environmental influence seemed largely uniform between species, often independently on genetic predictor. CII almost always significantly increased height RGR, D_{base} RGR, and $\log_{10}$(TLA) (see responses in *Figure 7* and model statistics in Appendix 6, *Table 7*). The only exception was *S. johorensis*' non-significant response in $\log_{10}$(TLA). Foliar phytochemical trait response to CII varied more between species, but were generally consistent across genetic predictors. When response was regressed on Soil, non-significant interactions from the Elevation models were dropped and significant CII effects appeared in *S. fallax*' foliar P (partial-R^2=0.05, β=-0.08, SE=0.04, t_{98}=-2.16, p=0.03) and *S. argentifolia*'s foliar K contents (partial-R^2=0.21, β=-2.44, SE=0.48, t_{98}=-5.04, p<0.01). The case for chlorophyll content seemed less complex; it decreased significantly from CII in both Elevation and Soil models in *P. tomentella* (partial-$R^2_{CII|Elev}$=0.04, $\beta_{CII|Elev}$=-4.69, SE=2.34, t_{104}=-2.00, p=0.048; partial-$R^2_{CII|Soil}$=0.04, $\beta_{CII|Soil}$=-4.73, SE=2.31, t_{104}=-2.05, p=0.04) and *S. fallax* (partial-$R^2_{CII|Elev}$=0.06, $\beta_{CII|Elev}$=-4.54, SE=1.68, t_{109}=-2.69, p=0.01; partial-$R^2_{CII|Soil}$=0.05, $\beta_{CII|Soil}$=-4.25, SE=1.70, t_{109}=-2.50, p=0.01).

In *S. johorensis*, all traits but total foliar N responded significantly to $\widehat{BA}$, in both Elevation and Soil models. No other species' trait expression was as plastic. *P. tomentella* only responded significantly in total foliar K, and then only in the Soil model. Independently on genetic predictor, *S. fallax*' D_{base} RGR, $\log_{10}$(TLA), and total foliar N responded significantly to $\widehat{BA}$. *S. argentifolia*'s total foliar N and K responded significantly in both Elevation and Soil models, but height RGR and mean SLA responses to $\widehat{BA}$ were only significant when predicted with Soil (see responses in *Figure 7* and model statistics in Appendix 6, *Table 7*).

Some sense of interspecific plasticity to vegetative competition (as $\widehat{BA}$) can therefore be determined from this data. *S. johorensis* responds dynamically in both physical and phytochemical traits; losing growth rates, while gaining SLA, and foliar P and K. And neither mother tree elevation nor soil seem to be dominant conduits for selection. *S. fallax* displayed some degree of plasticity, both in physical and phytochemical traits: also losing some growth, but gaining foliar N. Without any obvious bias for selection by mother tree elevation or soil quality. *S. argentifolia*'s – limited – plasticity, in contrast, seemed dependent on genetic heritage; Soil separated genetic from environmental effects on physical traits, Elevation did not. With losses in growth and foliar N due to $\widehat{BA}$, and gains in SLA and foliar K. And finally, *P. tomentella* barely responded at all, only in foliar K, whose response barely changed between genetic predictors (again, see responses in *Figure 7* and model statistics in Appendix 6, *Table 7*).

Multivariate progenic differentiation

All dipterocarp seedling traits (height and D_{base} RGR, log_{10}[TLA], mean SLA, mean foliar chlorophyll content, and total foliar N, P, and K contents) were standardized and, interspecifically, the progeny-wise multivariate Euclidean distances used as a metric of phenotypic differentiation. This extends the investigation of hypothesis 2 – the influence of Elevation and Soil on trait expression – into multivariate trait-space.

While accounting for plot-allocation, these distances produced significant variation in centroid location but not mean dispersion in *S. argentifolia* (PERMANOVA: partial-R^2=0.10, $\hat{F}_{5,\,87}$=2.14, $\hat{p}$=0.01; PERMDISP: $\hat{F}_{5,\,92}$=1.90, $\hat{p}$=0.10) and *S. fallax* (PERMANOVA: partial-R^2=0.07, $\hat{F}_{5,\,91}$=1.73, $\hat{p}$=0.02; PERMDISP: $\hat{F}_{5,\,96}$=0.37, $\hat{p}$=0.86), but neither in *P. tomentella* nor *S. johorensis*. All tests with 9999 permutations each.

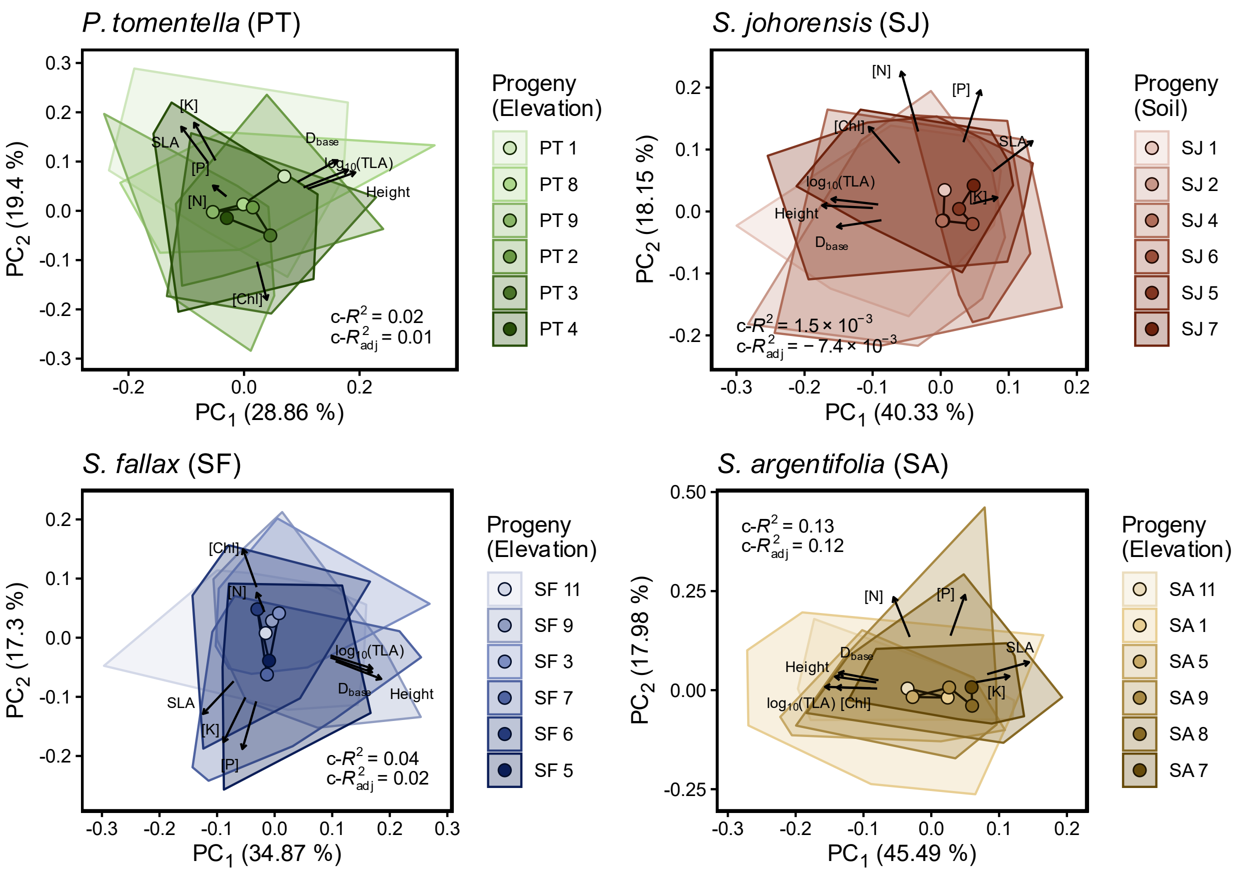

Figure 8. The first two principal components (PC_1 and PC_2) of dipterocarp seedling traits (Principal Component Analysis [PCA] on correlation matrices of height RGR [Height], D_{base} RGR [D_{base}], log_{10}[total leaf area] [TLA], mean SLA, mean foliar chlorophyll content [Chl], and total foliar N, P, and K contents). Showing convex hulls (polygons) around medians (points) with linear paths along ordinal mother tree elevation (Elevation) or soil quality (Soil), and genetic constrained-R^2 (c-R^2) and constrained-R^2_{adj} (c-R^2_{adj}). Progeny sorted, top to bottom, either from lowest to highest Elevation or Soil. n_{PT}=75, n_{SJ}=115, n_{SF}=102, n_{SA}=98. See loadings in *Table 3*.

From Euclidean *S. argentifolia* seedling trait-space, PC_1 responded significantly to both mother tree elevation (partial-R^2=0.08, $\beta=2.4\times10^{-4}$, SE=8.3×10^{-5}, t_{96}=2.90, p<0.01) and soil quality (partial-R^2=0.07, β=0.04, SE=0.02, t_{96}=2.68, p=0.01). PC_2 responded significantly to mother tree soil quality in *S. johorensis* (partial-R^2=0.04, β_{Soil}=0.02, SE=0.01, t_{112}=2.14, p=0.04). In *P. tomentella*, PC_2 almost responded significantly to mother tree elevation (partial-R^2=0.05, $\beta=-4.5\times10^{-4}$, SE=2.3×10^{-4}, t_{72}=-1.94, p=0.06). Neither PC_1 nor PC_2 responded significantly to either Elevation or Soil in *S. fallax*. Again, hypothesis 2 was supported, here in extended multivariate trait-space—though only partly. Constrained variance explained modeled with RDA (standardized Euclidean distances), and PC responses to Elevation and Soil modeled with identity link GLMs. Residuals approximately Gaussian and homoscedastic (see Appendix 4, *Figure 23*).

Only in *S. argentifolia* does there seem to be a clear differentiation along genetic predictors, both in mother tree elevation and soil quality—though elevation was a slightly stronger constraint (c-R^2_{Elev}=0.13 and c-R^2_{Soil}=0.10; see *Figure 8*). Along its genetic gradient, from low to high elevation and fertile to poor soil, mean SLA and total foliar K correlated noticeably positively, while mean foliar chlorophyll, $\log_{10}$(TLA), and height and D_{base} RGR correlated negatively (*Table 3*).

Table 3. Trait loadings (as Pearson correlations) in the first two principal components (PC_1 and PC_2) in *Parashorea tomentella*, *Shorea argentifolia*, *S. fallax*, and *S. johorensis* seedling trait-space (PCA on correlation matrices). Significant (p<0.05) linear genetic (either mother tree elevation or soil quality) effects on axes and traits in bold (see *Figure 7*).

Species	*P. tomentella*		*S. argentifolia*		*S. fallax*		*S. johorensis*	
Components	PC_1	PC_2	**PC_1**	PC_2	PC_1	PC_2	PC_1	**PC_2**
Traits								
Height RGR	0.84	0.28	**-0.78**	**0.12**	0.88	-0.24	-0.89	0.03
D_{base} RGR	0.70	0.36	**-0.74**	**0.15**	0.81	-0.20	-0.78	-0.08
$\log_{10}$(TLA)	**0.78**	**0.30**	-0.86	0.03	**0.81**	**-0.18**	**-0.82**	**0.07**
Mean SLA	-0.47	0.61	**0.79**	**0.24**	-0.60	-0.43	0.69	0.39
Mean [Chl]	0.17	-0.64	**-0.76**	**0.02**	**-0.26**	**0.50**	-0.54	0.47
Total [N]	-0.23	0.18	-0.30	0.80	-0.15	0.26	-0.30	0.78
Total [P]	-0.23	0.18	0.27	0.82	-0.27	-0.63	**0.30**	**0.67**
Total [K]	-0.38	0.64	**0.63**	**0.12**	-0.42	-0.59	0.43	0.08

Leaf symptom morphological species

Progenic differentiation in extended phenotypic structure

Leaf morphospecies community structure varied within one species, and so hypothesis 3 was partly supported. When controlling for plot-allocation, mean species richness ($F_{5,\ 104}$=2.82, p=0.02), Hill-Shannon ($F_{5,\ 104}$=2.89, p=0.02), and

Hill-Simpson ($F_{5,\ 104}$=2.53, p=0.03) all varied significantly between *S. johorensis* progeny. Modeled with two-way ANOVA, with controls for plot-allocation. Residuals approximately Gaussian and homoscedastic (see Appendix 4, *Figure 24*).

Modeling alpha diversity response, and model comparison

In order to deflate concurvity, and therefore to minimize explanatory redundancy, linear interactions had to be excluded for Hill diversity estimation. Genetic influence was modeled as only main effects – as either mother tree elevation (Elevation) or soil quality (Soil) – alongside CII and $\widehat{\mathrm{BA}}$. And additionally, AIC$_c$-favor determined whether CII×$\widehat{\mathrm{BA}}$ interactions should be included or not.

AIC$_c$ favored the Elevation and Soil models 6 times each, with consistent interspecific preferences: Elevation was always favored in *S. fallax* and *S. johorensis,* and Soil in *P. tomentella* and *S. argentifolia*. Consequently, in all three Hill diversities (D_0, D_1, and D_2), Elevation and Soil were both favored twice, depending on species (*Figure 9*).

ΔRMSE also favored Elevation and Soil 6 times each. And similarly to AIC$_c$-favor, there was no overwhelming bias in selection on Hill diversity, but

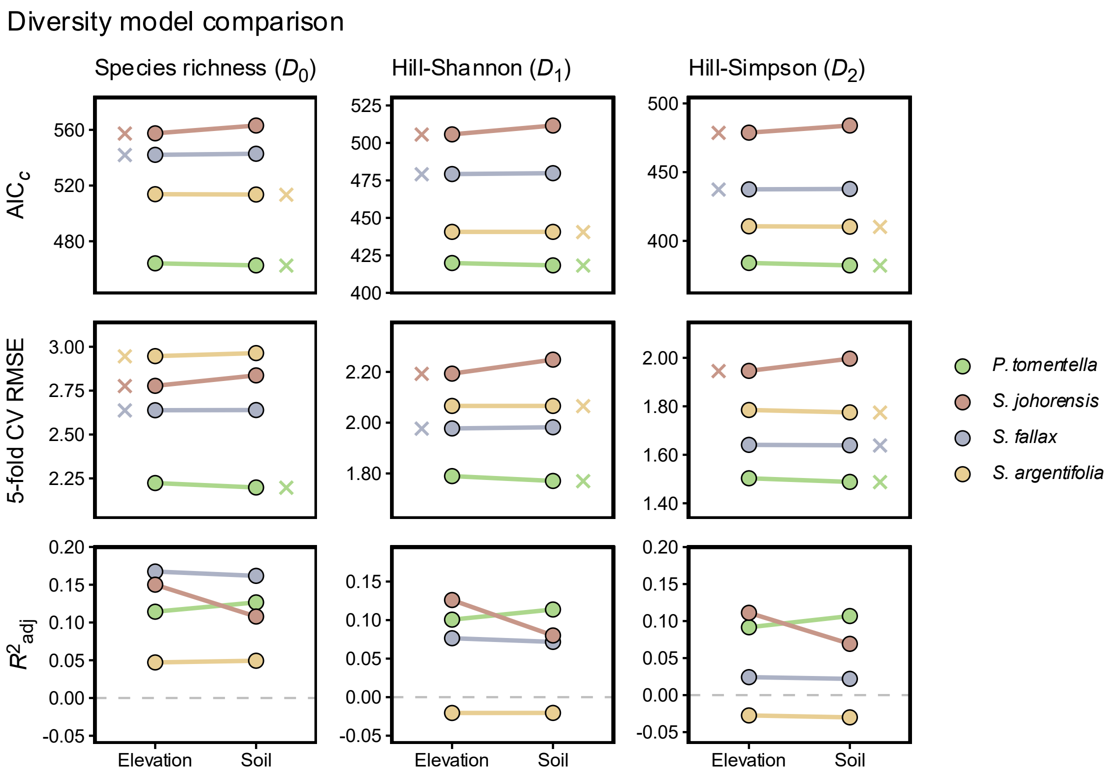

Figure 9. Model fit statistics (AIC$_c$, 5-fold cross-validated RMSE, and R^2_{adj}) for comparison of influence by mother tree elevation (Elevation) and soil quality (Soil) on species richness (D_0), Hill-Shannon (D_1), and Hill-Simpson (D_2). Colored crosses (×) indicate species-wise AIC$_c$- and 5-fold cross-validated RMSE-favor. Convergence in mean RMSEs were decent at 25 epochs (see Appendix 4, *Figure* 25).

interspecific favor was somewhat consistent (*Figure 9*). Relative RMSE-loss was always small however (all δRMSE≤0.025). With decent convergence across models at 25 epochs (see Appendix 4, *Figure 25*).

Influence of either mother tree elevation or soil quality, though noteworthy, was not strong enough to infer which was generally more significant among dipterocarps. In *S. johorensis*, however, it seems mother tree elevation might be a slightly stronger predictor of community diversity, independently on rarity-sensitivity, than mother tree soil quality.

Alpha diversity response to genetics

Hypothesis 4 was partly supported; mother tree elevation and soil quality influenced foliar community structure in *S. johorensis* (*Figure 10*). Its Elevation response always produced intermediate maxima in Hill diversity (D_0: partial-R^2=0.11, $F_{1.92,\ 1.99}$=6.85, p<0.01; D_1: partial-R^2=0.12, $F_{1.92,\ 1.99}$=7.05, p<0.01; D_2: partial-R^2=0.10, $F_{1.91,\ 1.99}$=6.01, p<0.01). Both AIC$_c$ and ΔRMSE favored the smooth-fit over an equivalent linear fit for all Hill diversities, though the relative differences were small (all δRMSE≤0.04). With decent convergence and consistent differences at 25 epochs (see Appendix 4, *Figure 26*).

In the Soil model, the response waned in Hill-Simpson. The Soil smooth generally did not produce a peak, and was not as strong as the Elevation response (D_0: partial-R^2=0.07, $F_{1.70,\ 1.91}$=3.04, p=0.03; D_1: partial-R^2=0.07, $F_{1.59,\ 1.83}$=3.07, p=0.03; D_2: partial-R^2=0.06, $F_{1.50,\ 1.75}$=2.54, p=0.06). AIC$_c$ favored the smooth-fit over an equivalent linear fit for species richness and Hill-Shannon, but a linear fit for Hill-Simpson. ΔRMSE favored the linear fit every time, though the relative differences were very small (all δRMSE≤6.7×10^{-3}). And favor essentially depended on epoch choice for species richness. With some convergence around 25 epochs (see Appendix 4, *Figure 26*).

When Hill diversity response was fit linearly, whether for Elevation or Soil, no other effects lost or gained significance compared to the smooth-fits. Though the Soil effect remained significant for all Hill diversities, Hill-Simpson included ($\beta_{D0|Soil}$=-0.78, SE=4.55, t_{114}=-2.23, p=0.03; $\beta_{D1|Soil}$=-0.68, SE=0.28, t_{114}=-2.44, p=0.02; $\beta_{D2|Soil}$=-0.56, SE=0.25, t_{114}=-2.25, p=0.03).

Additionally, genetic effects were highly valued by RF (see *Figure 10* and Appendix 6), but the models did not cover much of the variance (pseudo-$R^2_{D0|Elev}$=0.04, pseudo-$R^2_{D1|Elev}$=0.02, pseudo-$R^2_{D2|Elev}$=0.03; pseudo-$R^2_{D0|Soil}$=-0.02, pseudo-$R^2_{D1|Soil}$=-0.02, pseudo-$R^2_{D2|Soil}$=2.4×10^{-3}). The minimum node size per decision tree was 5, which should have allowed for enough splits to capture the same non-linear responses as the k=3 thin plate spline dimensions (n_{PT}=105, n_{SJ}=115, n_{SF}=113, n_{SA}=102). Perhaps the RF had issues capturing the sampled non-monotonic responses, and so lost predictive power as the population function folded on itself? This is a statistical issue I will not pursue further however.

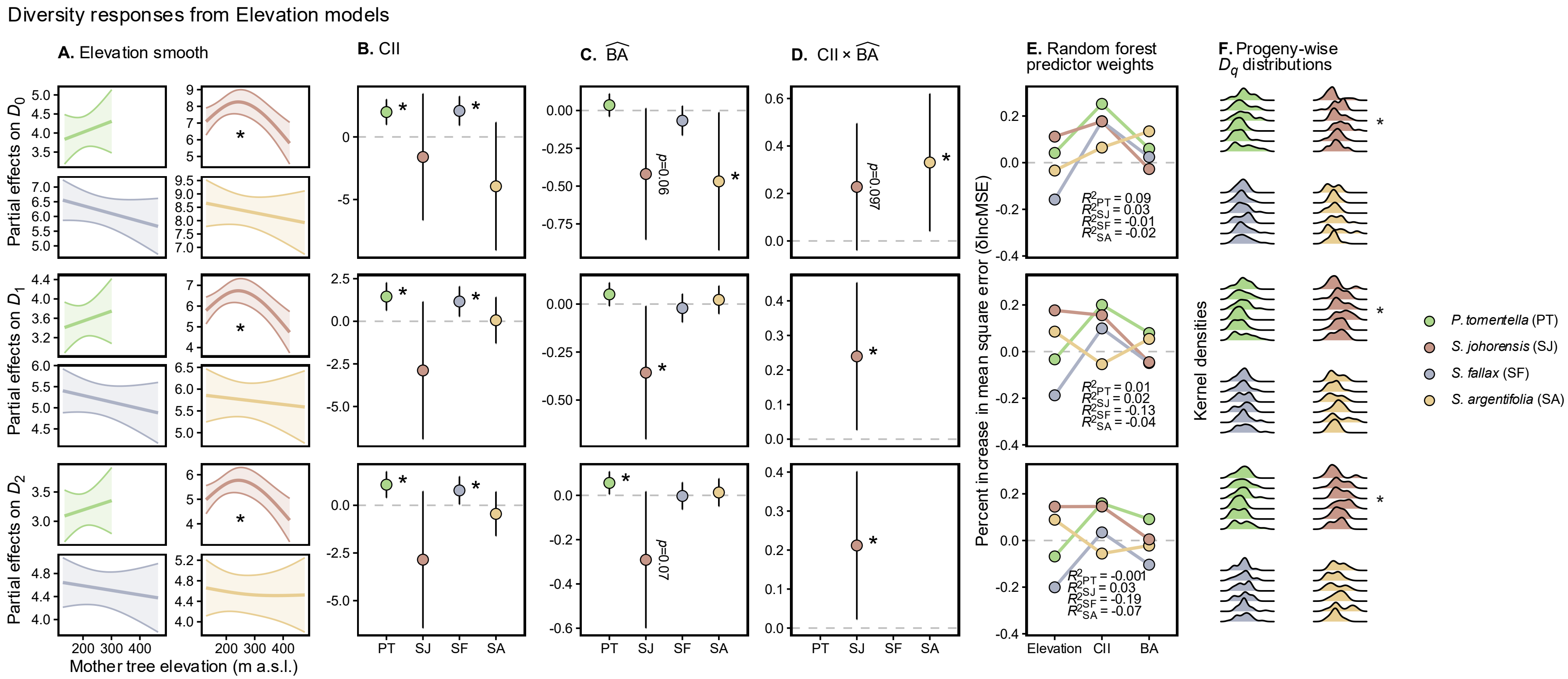

Figure 10. Partial effects on leaf morphological species richness (D_0), Hill-Shannon (D_1), and Hill-Simpson (D_2), from **A.** smooths (thin plate splines with k=3 dimensions for basis expansions each [see Wood 2022], partial effects from means in covariate space, fit with REML) from genetic effects (either mother tree elevation [Elevation] or soil quality [Soil, ordinally from fertile to poor]). And coefficients of **B.** CII, **C.** $\widehat{BA}$, and **D.** their interaction. All with 95 percent confidence intervals. Stars (∗) indicate significant (p<0.05) smooths and coefficients. And **E.** random forest predictor weights (δIncMSE) with their species-wise pseudo-R^2 (as R^2). Forests with 10000 trees, with 999 permutations each. n_{PT}=105, n_{SJ}=115, n_{SF}=113, n_{SA}=102. *S. fallax* Soil responses modeled with Generalized Linear Models (GLMs). All the others with Generalized Additive Models (GAMs). All with identity links. Residuals approximately Gaussian and homoscedastic (see Appendix 4; *Figure 27*, *Figure 28*, *Figure 29*, and *Figure 30*).

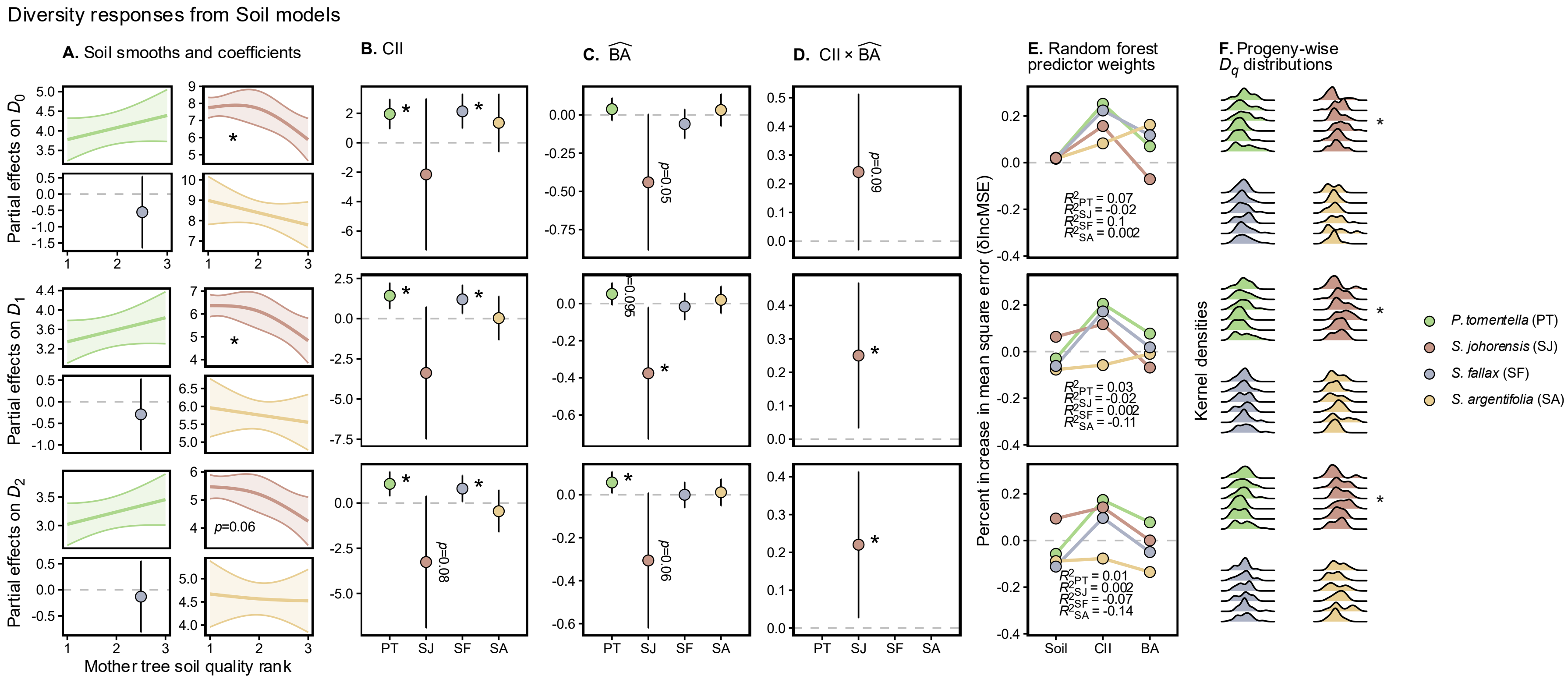

Figure 10. (continued)

Alpha diversity response to environment

Consistently, CII significantly increased Hill Diversity in *P. tomentella* (partial-$R^2_{D0|Elev}$=0.14, partial-$R^2_{D1|Elev}$=0.11, partial-$R^2_{D2|Elev}$=0.09; partial-$R^2_{D0|Soil}$=0.15, partial-$R^2_{D1|Soil}$=0.12, partial-$R^2_{D2|Soil}$=0.09; see other statistics in Appendix 6) and *S. fallax* (partial-$R^2_{D0|Elev}$=0.10, partial-$R^2_{D1|Elev}$=0.06, partial-$R^2_{D2|Elev}$=0.04; partial-$R^2_{D0|Soil}$=0.11, partial-$R^2_{D1|Soil}$=0.06, partial-$R^2_{D2|Soil}$=0.04; see other statistics in Appendix 6). In *S. argentifolia*, both the $\widehat{\mathrm{BA}}$ main effect (partial-R^2=0.04, β=-0.47, SE=0.23, t_{97}=-2.02, p=0.047) and the CII×$\widehat{\mathrm{BA}}$ interaction (partial-R^2≈0, β=0.33, SE=0.15, t_{97}=2.24, p=0.03) were significant predictors for species richness in the Elevation model. *P. tomentella*'s Hill-Simpson responded significantly positively to $\widehat{\mathrm{BA}}$, with both genetic predictors as covariates (partial-$R^2_{D2|Elev}$=0.09, $\beta_{D2|Elev}$=0.06, SE=0.03, t_{101}=2.14, p=0.03; partial-$R^2_{D2|Soil}$=0.09, $\beta_{D2|Soil}$=0.06, SE=0.03, t_{101}=2.21, p=0.03). Otherwise, only *S. johorensis* produced significant responses to either $\widehat{\mathrm{BA}}$ or the CII×$\widehat{\mathrm{BA}}$ interaction, which were always negative and positive, respectively (see *Figure 10* and Appendix 6).

Foliar community structure

Because of the novelty of investigation into extended dipterocarp phenotypes, elucidation of the observed structures, beyond the scope of the hypotheses, is merited.

While controlling for plot-allocation, multivariate centroid location varied significantly in leaf morphospecies community *Chao*-space between progeny of *S. argentifolia* (PERMANOVA: partial-R^2=0.09, $\hat{F}_{5,\,91}$=2.15, $\hat{p}$=0.01; PERMDISP: $\hat{F}_{5,\,96}$=0.71, $\hat{p}$=0.61), while mean dispersion varied significantly between progeny of *S. johorensis* (PERMANOVA: $\hat{F}_{5,\,104}$=1.55, $\hat{p}$=0.06; PERMDISP: $\hat{F}_{5,\,109}$=2.77, $\hat{p}$=0.02). The partial influence of progeny on multivariate community structure was similar in all four species (partial-R^2_{PT}=0.06, partial-R^2_{SA}=0.09, partial-R^2_{SF}=0.05, partial-R^2_{SJ}=0.06). All PERMANOVA $\hat{F}$-tests on marginal effects, with 9999 permutations each.

S. johorensis' GAM *F*-test (see *Figure 10*, **A.**) and PERMDISP results indicate that both alpha diversity (as Hill diversity) and beta diversity (as community Euclidean dispersion [Anderson et al. 2006]) vary as functions of genetic heritage. Community Euclidean dispersion was modeled equivalently to Hill diversity (with GAM) to investigate genetic effects on beta diversity. On the basis of its relative consistency in Hill diversity estimation (see *Alpha diversity response to genetics*), Elevation was chosen as the genetic predictor.

Both AIC_c and ΔRMSE favored the Elevation smooth-fit over an equivalent linear fit for community Euclidean dispersion (δRMSE=0.03), with decent convergence at 25 epochs (see Appendix 4, *Figure 31*). This smooth produced an inverse response to the Hill diversities, with an intermediate minimum, and was also significant (partial-R^2=0.09, $F_{1.88,\ 196}$=5.09, p=0.01). With Gaussian and homoscedastic residuals (see Appendix 4, *Figure 31*).

Since the multivariate centroid location did not vary significantly between progeny in *S. johorensis* (though permuted $\hat{p}$=0.06 was close to significance) and dispersion did ($\hat{F}_{5,\ 109}$=2.77, $\hat{p}$=0.02), linear community overlap does not seem like the most plausable explanation for the intermediate alpha diversity peak. In fact, obligate species (unique to progeny) richness clearly maximizes in one of the intermediate progeny (SJ 4, *Figure 11*). These varied a lot morphologically, including frequently observed miners, folders, and chewers, but also rare pupae, cocoons, eggs, hives, and galls.

It seems, the same progeny maximizing alpha minimize beta diversity; their tree-wise communities are, on average, rich in species but largely similar. Non-obligate species evenness (as Hill-Simpson [D_2]) increased in intermediate and decreased in

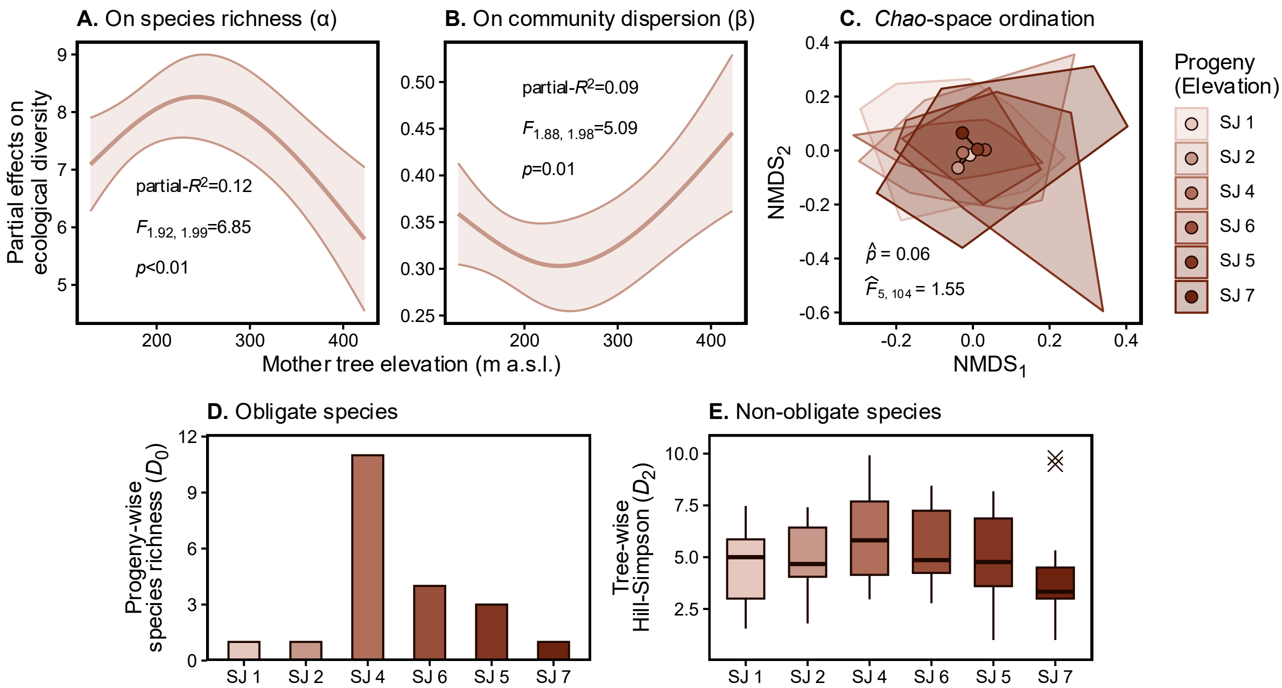

Figure 11. Leaf symptom morphological species community structure in *Shorea johorensis* Foxw. Progenic (as mother tree elevation [Elevation]) partial effects from Generalized Additive Models (GAMs) with identity links (thin plate splines with k=3 dimensions for basis expansions each [see Wood 2022], with partial effects from means in covariate space, fit with REML) on **A.** leaf morphospecies richness (D_0) as α-diversity proxy (same *S. johorensis* Elevation D_0 smooth for species richness from *Figure 10*, **A.**), and **B.** Euclidean distances from progeny-wise *Chao*-space medians (multivariate community dispersion) as β-diversity proxy. Both with smooth F-test results and 95 percent confidence intervals. With **C.** progeny-wise convex hulls and medians in 2D NMDS (Kruskal 1964) ordination (Stress=0.26, isotonic R^2=0.70), with PERMANOVA centroid location $\hat{F}$-test results. Also progeny-wise **D.** total obligate species (unique for progeny) richness (D_0), and **E.** tree-wise non-obligate Hill-Simpson (D_2) distributions (as boxplots). Progeny sorted, top to bottom and left to right, by increasing Elevation.

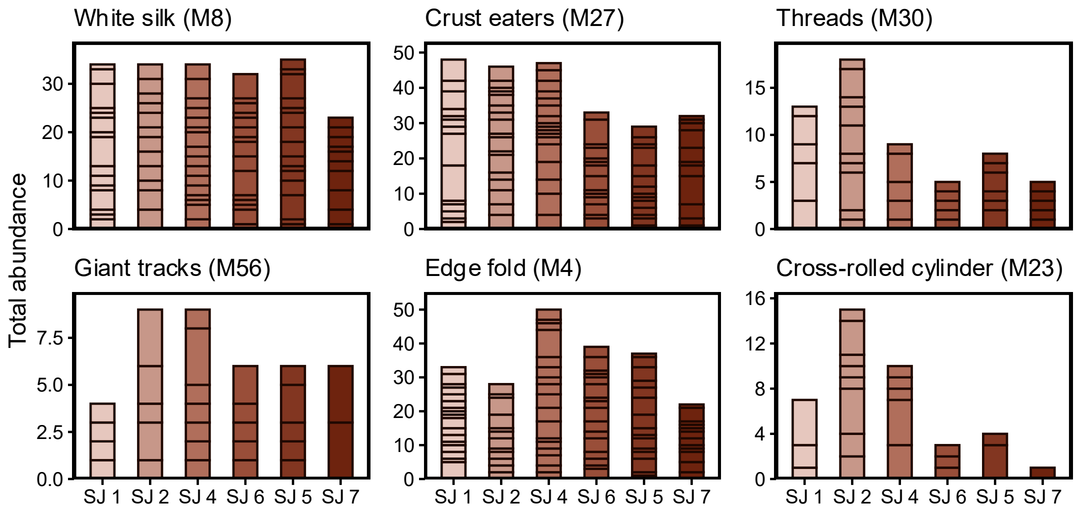

Figure 12. Progeny-wise total abundances of some leaf symptom morphological species in *S. johorensis*. Tree-wise abundances stacked. Progeny sorted, left to right, by increasing Elevation. See morphospecies descriptions in Appendix 7, *Table 9*.

the lowest (SJ 1 and SJ 2, 129 m a.s.l.) and highest Elevations (SJ 7, 423 m a.s.l.). Suggesting progenic community homogenization from common non-obligate species similarity out-paces the diversification from both rare obligate and common non-obligate species richness and evenness (see *Figure 10* and *Figure 11*). Even though all Hill diversity responses produced intermediate maxima, beta diversity (as dissimilarity) was still significantly smaller in these progeny (*Figure 11*, **B.**).

Across mother tree elevation, *S. johorensis*' leaf morphospecies densities varied. Some were uniform (M8 and M56) or close-to-uniform (M27 and M4), others left-tailed (M30 and M23) (*Figure 12*), but no morphospecies distribution was clearly right-tailed. Only rare (including obligate species) dependent much on the Elevation gradient. These were, generally, always absent in at least one, but usually multiple, progeny. This is consistent with the, largely, similar centroid locations (see NMDS in *Figure 11*, **C.**).

The response in diversity of leaf morphospecies to *S. johorensis* genetics was significant, but inconsistent, across ecological scales.

Constrained beta diversity

In order to test hypothesis 5, dipterocarp seedling trait influence on leaf morphospecies communities was investigated as constrained *Chao*-spaces with db-RDA (Legendre & Anderson 1999; Legendre & Legendre 2012b). Predictor redundancy and collinearity was investigated with SVD and VIFs prior to modeling. All traits (height RGR, D_{base} RGR, log_{10}[TLA], mean SLA, mean foliar chlorophyll, and total foliar N, P, and K) were included as constraints (all $SV_{PT} \geq 0.86$ and $VIF_{PT} \leq 2.46$, all $SV_{SA} \geq 1.03$ and $VIF_{SA} \leq 2.89$, all $SV_{SF} \geq 0.94$ and $VIF_{SF} \leq 3.37$, all $SV_{SJ} \geq 1.04$ and $VIF_{SJ} \leq 3.37$).

Adjusted total constrained explained variance (c-R^2_{adj}) was 2.00 percent in *P. tomentella*, 1.47 percent in *S. argentifolia*, 1.14 percent in *S. fallax*, and 1.23 percent in *S. johorensis*. $\log_{10}$(TLA) was the only significant constraint on leaf morphospecies community in *P. tomentella* (pseudo-$F_{1,\,66}$=1.63, $\hat{p}$<0.01). In *S. argentifolia*, height RGR (pseudo-$F_{1,\,89}$=1.20, $\hat{p}$=0.02), mean SLA (pseudo-$F_{1,\,89}$=1.19, $\hat{p}$=0.02), and total foliar N content (pseudo-$F_{1,\,89}$=1.14, $\hat{p}$=0.048) were all significant constraints. Mean SLA significantly constrained the communities in *S. fallax* (pseudo-$F_{1,\,93}$=1.71, $\hat{p}$=0.046). And in *S. johorensis*, $\log_{10}$(TLA) (pseudo-$F_{1,\,106}$=1.29, $\hat{p}$<0.01) and mean SLA (pseudo-$F_{1,\,106}$=1.27, $\hat{p}$<0.01) were significant constraints (*Figure 13*). Although influence was very weak (c-R^2_{adj} ≤0.02), hypothesis 5 was partly supported in all species; PES-traits significantly influence structure in extended dipterocarp foliar phenotypes. All permuted pseudo-*F*-tests

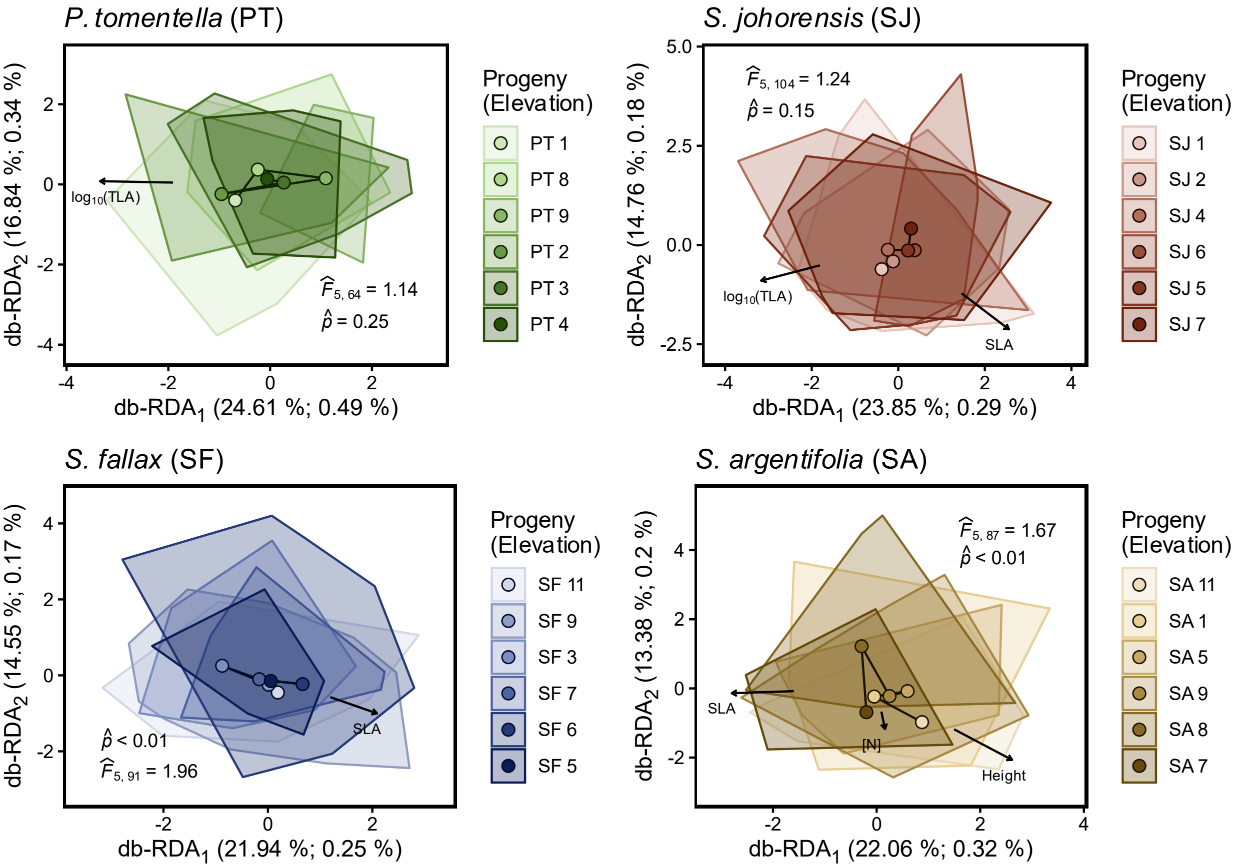

Figure 13. Chao-space ordination of leaf symptom morphological species in the first two principal constrained coordinates (db-RDA$_1$ and db-RDA$_2$) from Distance-Based Redundancy Analysis (db-RDA), with their variance explained (constrained; adjusted total). Showing convex hulls (polygons) around medians (points) with linear paths along ordinal mother tree elevation (Elevation). Significant ($\hat{p}$<0.05) constraining predictors as arrows. Results from PERMANOVA $\hat{F}$-tests on constrained centroid locations (no significant PERMDISP results). Progeny sorted, top to bottom, from lowest to highest Elevation. n_{PT}=75, n_{SJ}=115, n_{SF}=102, n_{SA}=98. See canonical coefficients in *Table 4*.

on marginal effects (eqn 13 in Legendre et al. [2011]), with 9999 permutations each. Residuals from db-RDA uncorrelated and independent (see Appendix 4, *Figure 32*).

When accounting for plot-allocation, within constrained leaf morphospecies *Chao*-space, centroid location varied significantly between progeny of *S. argentifolia* (PERMANOVA: partial-R^2=0.08, $\hat{F}_{5, 87}$=1.67, $\hat{p}$<0.01; PERMDISP: $\hat{F}_{5, 92}$=1.24, $\hat{p}$=0.31) and *S. fallax* (PERMANOVA: partial-R^2=0.08, $\hat{F}_{5, 91}$=1.96, $\hat{p}$<0.01; PERMDISP: $\hat{F}_{5, 96}$=0.65, $\hat{p}$=0.67). Again, suggesting that PES-traits have noteworthy influence on extended foliar phenotype community structure, supporting hypothesis 5. Significantly different unconstrained centroid locations and multivariate dispersion only in *P. tomentella* (PERMANOVA: partial-R^2=0.07, $\hat{F}_{5, 64}$=1.06, $\hat{p}$=0.04; PERMDISP: $\hat{F}_{5, 69}$=2.80, $\hat{p}$=0.02). *Chao*-space dissimilarities modeled as Euclidean distances between their corresponding principal coordinates. All PERMANOVA $\hat{F}$-tests on marginal effects, with 9999 permutations each.

In *S. argentifolia*, the first constrained principal coordinate (db-RDA_1) responded significantly to both Elevation (partial-R^2=0.05, β=-2.7×10^{-3}, SE=1.2×10^{-3}, t_{96}=-2.23, *p*=0.04) and Soil (partial-R^2=0.04, β=-0.50, SE=0.25, t_{96}=-2.02, *p*=0.047), with strong influence from $\log_{10}$(TLA), D_{base} and height RGR, mean foliar chlorophyll, total foliar K, and mean SLA (*Table 4*). No other significant Elevation or Soil gradients in constrained space. Residuals approximately Gaussian and homoscedastic (see Appendix 4, *Figure 33*).

Table 4. Canonical coefficients for the first two constrained (canonical) principal coordinates (db-RDA_1 and db-RDA_2) from Distance-Based Redundancy Analysis (db-RDA) of leaf symptom morphological species *Chao*-space constrained by dipterocarp seedling traits in *Parashorea tomentella*, *Shorea argentifolia*, *S. fallax*, and *S. johorensis*. Significant (*p*<0.05) leaf morphospecies community constraints and genetic effects on axes in bold (see *Figure 13* and *Figure 7*).

Species	*P. tomentella*		*S. argentifolia*		*S. fallax*		*S. johorensis*	
Constrained coordinate Constraint	db-RDA_1	db-RDA_2	**db-RDA_1**	db-RDA_2	db-RDA_1	db-RDA_2	db-RDA_1	db-RDA_2
Height RGR	-0.63	-0.06	**0.75**	**-0.59**	-0.74	-0.26	-0.79	0.03
D_{base} RGR	-0.43	-0.51	0.77	0.14	-0.62	-3.8×10^{-4}	-0.71	-0.07
$\log_{10}$(TLA)	**-0.96**	**0.02**	0.86	-0.12	-0.86	-0.44	**-0.90**	**-0.26**
Mean [Chl]	-0.03	0.85	0.60	-0.33	0.60	-0.29	0.73	-0.61
Mean SLA	0.08	-0.21	**-0.80**	**-0.04**	**0.16**	**-0.33**	**-0.45**	**-0.38**
Total [N]	-0.07	0.04	**0.05**	**-0.34**	0.30	-0.63	-0.29	-0.51
Total [P]	-0.21	0.35	-0.20	0.02	-0.04	0.12	0.28	-0.44
Total [K]	-0.04	0.02	-0.51	0.07	0.36	-0.28	0.32	-0.09

Discussion

Analytical linearity and implications of support in data

The hypotheses were constructed to produce a linear pathway for investigating influences from selection on dipterocarp PES trait-expression to these traits' influences on foliar communities. Under the assumption that climate change and pedogenesis are significant pathways for natural selection on dipterocarp populations, the support for hypothesis 1 and 2 implies that the expression of functional traits are predictable through relatively simple parameters (mother tree elevation and soil). And since hypotheses 3 and 4 were (partly) supported, climate change and pedogenesis extend their selection on dipterocarp foliar communities. The weak, but extant, support for hypothesis 5, then, provides a potential causal mechanism for this selection: functional traits regulate foliar niche spaces.

At some point, this linearity was broken by all species, except maybe *S. johorensis*. Although it did not produce significant univariate trait differentiation (failing to support hypothesis 1), the linear models clearly separated latent genetic effects in $\log_{10}$(TLA) and foliar P (*Figure 7*). Its morphospecies community centroid locations did not shift significantly in constrained trait-space (*Figure 13*) – tough almost in full community-space ($\hat{p}$=0.06) –, but community structure responded significantly to mother tree elevation (*Figure 10* and *Figure 11*). *S. argentifolia* progeny, on the other hand, did not produce response in community structure (*Figure 10*). But two of its significant constraints (height growth and SLA) responded to mother tree parameters (*Figure 7*), and mother tree elevation was able to explain a noticeable amount of variance in multivariate PES-trait-space (c-R^2=0.13). Meaning *S. argentifolia* broke analytical linearity by not supporting hypotheses 3 and 4. *P. tomentella* and *S. fallax* progeny also did not influence morphospecies community structure significantly. They did produce significant constraints ($\log_{10}$[TLA] and SLA), but only in *P. tomentella* did genetic heritage influence one of them ($\log_{10}$[TLA]) significantly. Neither *P. tomentella* nor *S. fallax* could support hypotheses 3 and 4.

This framework was not supported entirely. Responses appear in all analyses, but in different species. Although, if these dipterocarps can be considered ecologically equivalent (see Ashton [2004]), these findings do support the linear pipeline from adaptation to climate and pedogenesis all the way to functional trait influence on extended foliar niche spaces. If not, the suggested causal pathway still holds for *S. johorensis*. And since these trees were only seedlings, any observed effects are likely to amplify as they age.

Effects on seedling trait expression

Interpretations for management

S. argentifolia generally increased its height growth with mother tree elevation. D_{base} growth increased with poorer mother tree soil quality in *S. argentifolia* and *S. fallax*. And in *S. johorensis*, mother tree elevation decreased TLA, while in *S. fallax*, poorer mother tree soil quality led to increases. However, these genetic predictors also interacted antagonistically with light illumination, leading to equal respective increases and decreases (*Figure 7*). As a result, lowland progeny of *S. argentifolia* grew significantly faster than highland progeny, D_{base} growth increased in *S. argentifolia* and *S. fallax* progeny from fertile sites, and TLA increased in *S. johorensis* lowland and *S. fallax* fertile-soil progeny (*Figure 7* and *Figure 8*). In short, lowland and fertile-soil progeny grew significantly more acquisitively than their highland and poor-soil counterparts.

The conditions investigated here were realistic for a degraded dipterocarp forest, and so roughly represents cases in need of improving recruitment for the purpose of re-establishing phytosociological strata benefiting dipterocarps. No seedling was exposed to continuous sunlight, but grew beneath canopy with varying degrees of, primarily, lateral light exposure (see definitions in Table 2 in Clark & Clark [1992]). Priadjati (2002) found weaker growth responses in complete exposure than weak shade in *Shorea leprosula* Miq., which Ashton (2004:282–283) and Zipperlen & Press (1996) consider a light-demanding species. Likely some intermediate – interspecific – optimum exists for most (if not all) late-successional dipterocarps (see Poorter 1999), including the species investigated here. An open-field control could have produced a useful reference for maximum exposure. Nevertheless, for practical implementation, these results are not only valid, but useful. Any expected benefits from progeny selection in these traits in these (and probably similar) species may be nullified or lost completely if regeneration discounts light illumination. Clearly, then, management aiming to manipulate dipterocarp seedling performance – e.g. height and diameter growth – can benefit from intraspecific genetic selection, only, if environmental susceptibility is considered appropriately. And if controlled through artificial breeding, benefits from this selection are likely to compound (Grady & Axelsson 2023).

Light illumination seems ubiquitously significant for physical trait expression, and at least somewhat important for foliar traits. Basal area, on the other hand, produced interspecifically consistent varying response: *S. johorensis* seems to suffer the most from dense vegetation, *S. fallax* to some degree as well, *S. argentifolia* less so, and *P. tomentella* almost not at all. These results produce some insight into conspecific ecology. Indifference to vegetative competition, here, suggests that seedlings are resilient to overstorey density. On the other hand, if responses are significant, this points towards density-dependency. Such seedlings might be more difficult to establish if recruitment (of all plants) is large, as they would likely require more maintenance for similar yields. Which is a reasonable concern when restoring degraded dipterocarp forests with many fast-growing pioneer species, such as *Macaranga* Thouars spp. (Hector et al. 2011; Axelsson et al. 2024). However, given the uniformity in seedling survival (Appendix 6, *Figure 34*), it seems like increased susceptibility would not lead to mortality, but simply, reductions in acquisitive traits (i.e. height and D_{base} growth, and TLA). When basal areas are large, selecting certain species for restoration – specifically, re-establishment of dipterocarp-dominated canopies – might be worthwhile, especially if returns are expected expeditiously. This echos Axelsson et al. (2022), who found foliar beetle richness to increase on selected over random tree hosts. These findings are significant for restoring dipterocarp phytosociological primacy, whether for conservational or commercial purposes.

Congruence with the global plant economic spectrum

Phytochemical trait relationships mostly adhered to the global PES (Wright et al. 2004; Reich 2014). In *S. fallax*, however, chlorophyll content was negatively related to all the primary acquisitive traits: height RGR (r=-0.28), D_{base} RGR (r=-0.18), and $\log_{10}$(TLA) (r=-0.08). If leaf and stem trait economics are truly independent (see Baraloto et al. 2010), this might simply be a consequence of conspecific environmental sensitivity. Although *S. fallax*' height RGR, D_{base} RGR, and $\log_{10}$(TLA) all responded positively to light illumination (CII), its foliar chlorophyll content responded negatively. Axelsson et al. (2021) found not only dipterocarp seedlings in general, but *S. fallax* in particular, to be sensitive to drought events. Perhaps more than the other species investigated here, *S. fallax* might suffer from excessive illumination. Only in $\log_{10}$(TLA), the weakest negative link to chlorophyll, was there a significantly negative interaction between *S. fallax*' genetics and light illumination (Soil×CII, *Figure 7*). Implicitly, then, these species' chlorophyll content and growth rates only co-varied positively when genetic heritage managed to off-set the negative chlorophyll-light illumination relationship, as in *S. argentifolia* (see genetic×CII effects in *Figure 7* and PC-loadings in *Figure 8*). Given what is known of two boreal and temperate canopy trees (Yang et al. 2020), this points towards possible interspecific differences in molecular regulation of environmental sensitivity.

Plant tissue K content correlates strongly with efficient drought response in *Eucalyptus* clones, such as up-regulating PSII electron transport to prevent photoinhibition (Santos et al. 2021). And as a primary regulator of cell swelling (Mohr et al. 1995), foliar K availability might improve stomatal control of severe water potentials (Freitas 1997). In *S. argentifolia* and *S. fallax*, foliar K decreased with light illumination. Progeny of *S. argentifolia* were able to off-set this loss through genetic means, *S. fallax*' were not (*Figure 7*). These species' phytochemicals clearly respond differently to varying degrees of light and shade. Controlled investigation into photoinhibition and xylem cavitation, potentially exacerbated obstacles in youth (Axelsson et al. 2021), might shed more light on genetic ties to phytosociology and therefore ecological function. Naturally, these mechanisms extend into resilience, particularly for drought (Freitas 1997). And since foliar K response globally favored the soil model (*Figure 6*), progeny selection based on mother tree soil quality might advance forest management in this direction.

Disagreement with the global plant economic spectrum

A global PES is valuable, but each system requires contextualized analysis. What produces conservative strategies in the Cerrado (Maracahipes et al. 2018) or Serengeti (Mohanbabu et al. 2023) likely will not in Bornean dipterocarp forests—simply because droughts are rare here. And when the region experiences them, both historically and contemporarily, habitats change on large scales for long times (Goldammer et al. 1996; Ashton et al. 2021; Axelsson et al. 2021). In xerophytic environments, plants might strategize acquisitively under canopy (Maracahipes et al. 2018; Mohanbabu et al. 2023). On the contrary, in these closed humid forests, growth responds strongly to light illumination (see *Figure 7*).

This is not to say that exposure cannot hurt dipterocarp seedlings; mortality decreases already in weak light (Philipson et al. 2014), and the CII never exceeded 3 ("10-90% of the vertical projection of the crown exposed to vertical light" [Clark & Clark 1992]), with a maximum of 5 ("Crown completely exposed (to vertical light and to lateral light within the 90° inverted cone ecompassing the crown)" [Clark & Clark 1992]). But in this common garden, which – realistically – simulates natural recruitment conditions, these dipterocarps, intraspecifically, acquired acquisitive strategies (i.e. fast growth) when under selection pressures typical of drier lowland environments with fertile soils. And conservative strategies (i.e. slow growth) when shaded and under selection of wetter uphill conditions (*Figure 7*).

Maracahipes et al. (2018) note that SLA increases in shaded conditions and determine this to be acquisitive behavior, because in the Cerrado, the alternative is semi-arid open savanna. In these dipterocarps, similarly, SLA always decreases with light illumination and sometimes increases with vegetative competition, which I, in contrast, must determine to likely be a conservative strategy. Partly because SLA increases either orthogonally or antagonistically to the primary acquisitive traits (height RGR, D_{base} RGR, and log_{10}[TLA]), and partly because the alternative environment is vacant rainforest gap. Globally, SLA increases with shade (Hodgson et al. 2011). Perhaps some intermediate value of SLA produces a global acquisitive peak, which might lie between the minima reported here and maxima in Maracahipes et al. (2018) and Mohanbabu et al. (2023).

Foliar N, P, and K varied similarly in these dipterocarps: they all decreased with light illumination (*Figure 7*). Though due to the, either, orthogonal or antagonistic relationships to acquisitive traits (*Figure 8*), these phytochemicals must either not have influenced resource economic strategy or actively implicated conservative strategy. These differences do not seem to be entirely reducible to climatic conditions however. In the same area, close to this common garden, Axelsson et al. (2022) measured and pooled trait correlations between 24 planted native tree species (not only, but majority, dipterocarps) and found acquisitive alignment in SLA and foliar N, congruent with the global PES (Wright et al. 2004; Reich 2014). Both *P. tomentella* and *S. fallax* were included in their trait decomposition, but neither *S. johorensis* nor *S. argentifolia*. However, similarly to the dipterocarps investigated here, and contrary to Baraloto et al.'s (2010) neotropical trees, Axelsson et al.'s (2022) foliar K aligned well with conservative strategy (wood density and slow growth).

These discrepancies highlight three things: (1) plant economic strategy seems to change when light hurts plant fitness through excess contra absence, (2) the intrinsic reduction in suggesting plant traits respond to strategy and not ecophysiology may confound cause and effect, and (3) intraspecific PES trait-relations vary noticeably between humid tropical species, even within sub-families (Dipterocarpoideae). Reich (2014) reasons that light-saturated photosynthetic capacity increases proportionally with SLA. Consequently, when SLA grows in plants with conservative strategies, as – arguably – in these *S. argentifolia* seedlings, their leaves must not be light-saturated. Increasing SLA could simply be a response to harvest what limited light is available. As the seedlings mature, then, SLA-alignment might change towards acquisition. Negative correlation between SLA and resource acquisition (i.e. fast growth) might therefore offer an index for system light limitation.

Interactions between genetic predictors and light illumination on $\log_{10}$(TLA) varied from positive to negative between species (*Figure 7*). Suggesting that total leaf area depends more on conspecific strategy than environmental inputs. This seems reasonable, given the perhumid conditions across the environmental range sampled, which dominates on the island. As abiotic variance minimizes, the niche space responsible for plant economic acquisition and conservation through stress shrinks; environmental constraints are alleviated and species are free to adapt in more directions. The question then becomes: where do these trees find vacant slots? And, perhaps more importantly: as climates change and lowland environments move towards xerophication (Axelsson et al. 2021; Pang et al. 2021; Colwell & Feeley 2025), which of these evolutionary "freedoms" would doom what species into extinction?

Climate change and dipterocarp genetics

A, growing, concern for these forests and their management are climate change impacts. Since elevation proxies climate change, which has been predicted to significantly impact dipterocarp distributions in the near future (Pang et al. 2021; Colwell & Feeley 2025), and is already contributing to extreme weather events (Goldammer et al. 1996; Axelsson et al. 2021), these, and similar, results might prove to be useful guides in managing forest resilience. And although steps have been taken to illuminate effects from climatic gradients (Priadjati 2002; Axelsson et al. 2023), much uncertainty remains. For one, do all dipterocarpoids respond similarly? There are 162 species endemic to Borneo alone (Bartholomew et al. 2021). Unravelling their conspecific susceptibilities to even a few stressors would not only be time-consuming, but require significant strides in effort. Additionally, long-term trials are lacking. These data reflect the early lives of immature seedlings, still beneath the understorey. Would these responses subsist through time? Likely not. Priadjati (2002) found that physical traits in *S. leprosula* respond differently both to and through time. The data presented here might aid in improving prediction. Though as recent research has declared, there is a desperate need to invest many more resources in this direction (Axelsson et al. 2020; Bartholomew et al. 2021; Grady & Axelsson 2023).

Mother tree elevation, consistently, correlates negatively with Fick & Hijmans' (2017) interpolated mean annual temperature and daily incident solar radiation, but positively to mean annual precipitation (*Table 1*). Highland environments would, therefore, generally select for progeny best adapted to cooler and wetter conditions, and *vice versa*. Simply moving lowland progeny uphill might not suffice if they do not adapt well to increased precipitation. Highland progeny, on the other hand, might not deal well with increased temperatures. Through pre-adaptive cross-breeding, some maximally fit genotypes might be developed by selecting on combinations of stressors, i.e. increased temperatures and precipitation. And in extension, relationships to invertebrate communities sensitive to the same parameters (Boyle et al. 2021) maintained.

Since these climatic parameters are subject to change, intense novel natural selection might lead to overall reduced fitness (again, also in extended phenotypes [Boyle et al. 2021]), or even worse, progenic extinction. And considering the Indian dipterocarps' likely Pliocene extinctions through xerophication (Ashton et al. 2021), such premonitions are not only less-than alarmist, but realistic. Climate change-induced xerophication, extreme weather events (Goldammer et al. 1996; Axelsson et al. 2021; Pang et al. 2021), with subsequent biotic attrition (Colwell & Feeley 2025), and deforestation in Bornean lowlands (Bartholomew et al. 2021; Danylo et al. 2021), are predicted to intensify and continue in the near-future. Assisting in cross-breeding and progenic migration might limit related losses, as already suggested by Grady & Axelsson (2023). And since drought-related resilience likely increases with age in dipterocarps (Axelsson et al. 2021), these proposals demand some urgency.

Investigation into the genome of *S. leprosula* has highlighted the role of infrequent drought in molecular selection on humid dipterocarps (Ng et al. 2021). Such latent adaptation may be utilized only through continued genetic research. Very likely, other dipterocarps also up-regulate certain genes in response to drought simulation. Outstanding progenies may be found through irrigation treatments and trialed in common garden experiments. Conserving the genetic diversity, and therefore ecological functions, of lowland progeny might not only improve conservation, but also increase resilience of what highland forests manage to survive the weft of their contemporary threats, and subsequently, facilitate future restoration of lowland dipterocarp forests.

Extended foliar phenotypes

Environmental effects on community structure

Community responses to basal area are difficult to interpret. This is due to the ephemeral nature of the statistic. High basal area could imply small but many or few but large stems. As such, it both describes a young and an old stand simultaneously. If we imagine that old trees produce community spill-over to smaller seedlings, we would think that Hill diversity should respond positively. But if we interpret high basal area as a young and dense stand, we might imagine that extended phenotypes would homogenize, and that the net effect of basal area should lean towards reducing Hill diversity—maybe less so as insensitivity to rare species (q) decreases. Both seem to have happened in different species. $\widehat{\mathrm{BA}}$ produced negative effects in *S. argentifolia* and *S. johorensis*, though they were only significant for species richness (q=0) and Hill-Shannon (q=2), respectively. In *P. tomentella*, on the other hand, Hill-Simpson increased significantly with $\widehat{\mathrm{BA}}$ (*Figure 10*). Since centroid locations and multivariate dispersion only differed significantly between *P. tomentella* progeny, this environmental heterogenization of morphospecies communities did not affect its progeny uniformly. Instead, sensitivity to heterogenization varied between progeny. And if the positive response scales the intermediate Hill-Simpson peak along mother tree elevation, we can imagine that differences in beta diversity are amplified.

Light illumination increased Hill diversity, both as a single main effect in *P. tomentella* and *S. fallax*, and in interaction with basal area in *S. johorensis* and *S. argentifolia* (*Figure 10*). It is tempting to consider stand conditions with high illumination and large basal areas as rich in old trees and therefore with spill-over potential. However, since light illumination increased total leaf area in all four species (*Figure 7*), this effect is more likely a consequence of higher probability of foliar exploitation. Also, given invertebrate sensitivity to temperature (Boyle et al.

2021) and the use of pseudo-species here (leaf morphospecies), speculating on the influence of light illumination on community structure from this data should perhaps be discouraged. And since $\widehat{\mathrm{BA}}$ includes non-dipterocarps, even the mahoganies, responses to $\widehat{\mathrm{BA}}$ cannot be considered entirely valid for native dipterocarp systems. Again, responses reflect the conditions of the design and should not be extrapolated.

Nevertheless, these results could suggest that the relative strengths of the two basal area-effects – of spill-over and homogenization – vary interspecifically. Both would be present in all dipterocarp species, but in *S. johorensis*, homogenization was dominant, while *P. tomentella* experienced enough spill-over to off-set the homogenization. This is not an unreasonable interpretation, since mono- and oligophagy are common among phytogaphous insects (Schoonhoven et al. 2005:6–9) (and many leaf morphospecies only occurred on few dipterocarps and their progeny [data not shown]). Therefore responses would depend much on conspecific insect biology. Unfortunately, since only proxies to species were inventoried (leaf symptoms), any analyses of specialist-generalist compositions were not possible, and so no related hypotheses could be tested.

Foliar community structure in *Shorea johorensis*

The obligate (unique to progeny, or non-shared) species richness grew proportionally to total abundance (data not shown), in all progeny. Meaning, the populations of each obligate species were approximately equally frequent in their respective progeny. There were simply more in SJ 4, whose richness peak likely explains the intermediate maximum in the alpha diversity smooths (at least D_0, see *Figure 10*). But not the minimum in beta diversity. Non-obligate (or shared species) evenness maximizes across intermediate progeny (SJ 4, SJ 6, and SJ 5) (*Figure 11*). The individuals of these progeny are rich in species, which are also evenly distributed. But they are, on average, relatively similar.

Response in species richness indicates that progeny selection in artificial regeneration may impact the availability of rare-species substrate. And it seems that this might happen, primarily, because of intraspecific host-specificity (i.e. in obligates). Some morphospecies seem to prefer certain *S. johorensis* genotypes; a few of them have a proclivity to host many more rare species than the others (2.75- to 11-fold differences [see *Figure 11*, **D.**]). Neither seedling trait-space centroid location nor dispersion differed significantly between *S. johorensis* progeny however, and so this discrepancy does not seem reducible to the PES-traits investigated here. Identifying phytochemicals in more detail (beyond total elementary contents) might discover molecular insect-plant dependencies. Additionally, the community similarity-gradient along mother tree elevation (*Figure 11*) follows empirical prediction: extended communities produce gradients of similarity as a function of genetically influenced phenotypic expression.

Effectively, community structure varies over genetic ecotones (as in Whitham et al. 1994, 2006; Dungey et al. 2000; Bangert et al. 2006).

As elevation and topographical complexity increase, dipterocarp populations scatter (Symington 1943:xii–xxiii; Aiba & Kitayama 1999), their gene flow is inhibited, and they differentiate genetically (Grady & Axelsson 2023). Consequently, extended communities should vary noticeably between highland and lowland progeny. This data cannot, either, support or oppose this prediction, since all the seedlings' native communities were not sampled, only lowland communities were (the common garden is located 130 m a.s.l.). This discrepancy, between highland progeny and lowland community, might have limited the observed rare species on SJ 7 (from 423 m a.s.l.). And similarly, its observed increase in beta diversity can reasonably be explained by the expected unfamiliarity to the communities native to lowland systems. This would produce extended foliar phenotypes largely influenced by the whims of environment and not genetics.

It is interesting, then, that progeny from altitudes similar to the common garden's (SJ 1 and SJ 2, both from 129 m a.s.l.) did not maximize alpha diversity. Intermediate progeny did (SJ 4, from 221 m a.s.l.). This casts some doubt on the assumed positive effects from progeny-garden similarity. If dipterocarp genetics truly influences foliar community structure, it is not unreasonable to imagine that progenic introductions would expand niche spaces, even marginally. First, these might not have reached maximum expansion until the trees become mature, and second, might not be filled entirely in less-than four-year-old seedlings—even in Bornean dipterocarp forests (this requires investigation). The simplest solution to the problem of interpreting these alpha diversity responses seems to be accepting some genotypic favor in certain (few) foliar species.

Analyses into species-wise distributions over proxies to genetic similarity (e.g. mother tree elevation) can highlight ecological mechanisms at species-scale by mapping specialist and generalist densities, as well as argue for community genetics as a cause for differentiation (Whitham et al. 1994). These are useful because they can give insight and guide investigation into causal mechanisms, such as metabolic dependency and interaction (Dungey et al. 2000). And could inform theories on communal evolution. For instance, by mapping species densities along niche gradients to find adaptive fringes (e.g. MacArthur 1965). However, making these kinds of claims require two things this data cannot produce: functionally meaningful species as response, and insight into their specific biology. Only pseudo-species were inventoried (morphological species), and so, analytically, this data is approaching its limit.

Two morphospecies displayed obvious preferrences for lower mother tree elevation (M23 and M30, see *Figure 12*), and another almost a unimodal distribution maximizing intermediately (M4, see *Figure 12*). This is hardly enough to consider mother tree elevation a significant genetic ecotone. Although, responses ought to amplify as the seedlings mature, and present themselves when functional groups are inventoried in place of their proxies. It seems, anyway, that these morphospecies respond to dipterocarp genotype.

Axelsson et al. (2022) sampled beetles (Coleoptera) from understorey dipterocarp canopies and identified them to family-level and feeding guilds. Not only would beetle families have been able to tell of true community composition, but phagy about trophic dynamics. Tying trait-constraints on communities of feeding guilds would, subsequently, be able to guide investigation in much more detail. What foliar traits promote herbivores and fungivores, or saprophagous and xylophagous beetles? And at what life stages: while living or decomposing? If the inventoried species represent meaningful functional groups (say, phagy), much can be inferred about trophic interaction, but clearly also more broadly about ecosystem regulation—especially if above and below-soil communities (e.g. mycorrhizal, see Peay et al. [2010]) are sampled in synchrony. And when species of phytochemicals are functionally identifiable, metabolic interactions can be inferred with some confidence too (Dungey et al. 2000).

Genetic dependencies in extended communities

Even though *S. johorensis*' constrained principal coordinates (db-RDA$_1$ and db-RDA$_2$) did not produce a significant response to either mother tree elevation or soil quality, the progenic multivariate medians did shift locations linearly to both ($r_{\text{Elev×db-RDA1}}$=0.64, $r_{\text{Elev×db-RDA2}}$=0.98, $r_{\text{Soil×db-RDA1}}$=0.56, $r_{\text{Soil×db-RDA2}}$=0.82, n=6, see *Figure 13*). And, as already established, neither alpha nor beta diversity responded linearly to either (*Figure 10*). More interestingly, both TLA and SLA significantly constrained its morphospecies communities. TLA aligned well with height and diameter growth, and is itself considered an acquisitive trait (Wright et al. 2004; Reich 2014). SLA, instead, aligned itself in the opposite direction, towards conservation (see *Figure 8* and *Table 3*). And, not surprisingly, they constrained the leaf morphospecies communities antagonistically (see *Figure 13* and *Table 4*). *P. tomentella*'s TLA constrained morphospecies community composition. And in *S. argentifolia*, SLA and height growth constrained communities antagonistically (see *Figure 13* and *Table 4*). Since all these traits were significantly influenced by mother tree elevation and soil quality (*Figure 7*), and most of them well-aligned with the PES, there are multiple links from dipterocarp genetics to foliar community structure, with ties to functional ecology.

Because the constraints' explained variance was so small (all c-R^2_{adj}≤0.02) and light illumination and basal area seem dominant on most trait expressions (see RF δIncMSEs in *Figure 7,* **E.**), a large proportion of the total effect must be due to the environment. Although, the traits investigated here are only a subset of the potentially constraining functional traits, and so do not represent all of the host's trait-influence. Elementary contents are severe reductions of metabolic processes, and no leaf thickness or resistance to tearing was estimated. Nevertheless, seeing clear patterns in constraining seedling traits provides opportunity for investigating temporal changes in influence on extended foliar dipterocarp phenotypes. It is reasonable to assume that seedlings produce only marginal influence on foliar communities, partly due to expected spill-over from larger trees, partly due to their exacerbated dependence on the environment in youth (e.g. Axelsson et al. 2021). Consequently, their influence on extended communities (constrained-R^2_{adj}) ought to increase with age. Through repeating these analyses, and comparing temporally paired observation, this hypothesis is testable.

Relevance for tree breeding

Acquisitive traits are often endorsed for restoration-oriented management (Banin et al. 2022) and are typically the sole phenotypic traits under artificial selection in forest tree-breeding programs. Even in the context of pre-adaptive resilience-breeding, the ubiquituous purpose is to retain growth for industrial ends (e.g. Namkoong et al. 1988; Rosvall & Lindgren 2012; Savill 2019; de Oliveira Castro et al. 2021). Neglect for downstream effects from manipulating these traits could clearly have impacts on extended phenotypes and therefore ecological functioning beyond tree physiology. Both in theory (Whitham et al. 2003, 2006) and in practice (Martinsen & Whitham 1994; Whitham et al. 1994; Benoit & Askins 1999; Dungey et al. 2000; Treseder & Vitousek 2001; Saltonstall 2002; Bailey et al. 2006; Axelsson et al. 2022).

Lindh et al. (2024) found – interspecifically – conservative traits to maximize profitability in dipterocarp management (including *P. tomentella* and *S. fallax*). Here, intermediate *S. johorensis* strategies maximized foliar alpha diversity (Figure 8, Figure 10, and Figure 13). And Axelsson et al. (2022) found beetle diversity (as ln[D_1]) to be positively correlated with conservative traits in pooled tree compositions (including *P. tomentella* and *S. fallax*). Since both acquisitive and conservative traits influenced foliar community structure in *S. johorensis* and *S: argentifolia* (*Figure 13*), selection in either direction should influence their alpha diversity. Thus, breeding these dipterocarps towards conservativeness might maximize profits (Lindh et al. 2024) and empoverish insect communities simultaneously. Some intermediate trait-combination could, perhaps, benefit both economic and ecological ends. And so, there seems to exist some trade-off in breeding dipterocarp seedlings for commerce and conserving extended phenotypic diversity, which differs interspecifically.

Communities evolve in aggregate, and their genetics are interdependent (Whitham et al. 2006). As selection coerces dipterocarp populations to float between their respective ends of resource economic spectra, their foliar communities shrink and expand at the behest of niche spaces, weaving and folding through time. It is no longer adequate to consider genomes as conspecific entities;

genes change through selection beyond populations. Therefore, as dipterocarp genetic diversity continues to degrade, cascades bereaving substrate for their extended foliar phenotypes ought to be expected. My results extend the empirical evidence supporting ecocentric, and not phytocentric, approaches to plant-breeding.

Design limitations and suggested improvements

Phenotypic models

Since progeny were selected to maximize elevation ranges only, without concern for soil collinearity, their partial influences on trait evolution could not be tested. This means that these models, like others (e.g. Tito de Morais et al. 2015), only provide heuristic guidance for ranking selection factors, not definitive empirical support for theory. This happened because Acres et al.'s (1974) Sabahan soil map was found after the inventory was conducted—originally, elevation was the only genetic predictor under consideration. Elevation and soil could be selected to, simultaneously, maximize ranges and minimize collinearity. For instance, by keeping covariance under some threshold. This would improve modeling and potentially allow for separating partial influence.

The quality of Acres et al.'s (1974) data is additionally uncertain; mother tree-wise soil inventories should provide data with greater predictive power. Ong & Kleine (1995) found their data useful, but only in the sense that it improved modeling. As far as I am aware, no formal quality analysis has been conducted on Acres et al.'s (1974) maps. And since soils change, there are some concerns regarding their age too. However, if the soil categorization was conducted on reasonable scales, they should still, at least roughly, represent pedogenic selection. (Natural selection happens over large temporal scales; the past condition of these soils have had an impact on contemporary phenotypic expression. In fact, this is implicitly assumed by the modeling.) Data on topsoil pH, cation exchange capacity, base saturation, and texture would have provided much more useful soil quality proxies, but also more genetic predictors. Detailed analyses require detailed data.

Sampling more progeny would not only, potentially, provide larger mother tree parameter ranges, but also fill the gaps in these models. Expanding environmental gradients is important for conducting inference on dipterocarp evolution, but interpolated predictions need to be checked when models are built on sparse data. There is room to improve these models and to test their interpolated predictions, and as usual, it simply requires more data.

Common garden site-effects

Common gardens are used to equalize environmental influences. But since environments select on genotypes, some would systematically be more fit for the environment of the common garden. These kinds of site-effects could be accounted for easily enough with multiple common gardens—preferably in environments that, as closely as possible, resemble the mother trees'.

This common garden matched the elevation of the lowland progeny (around 130 m a.s.l.), which were, generally, the most acquisitive in the three *Shorea* species. At higher altitudes, they might still respond acquisitively if this is what their genotypes code for, though their mortality should increase from novel stress (Reich 2014). Also, since foliar traits depends on edaphic conditions (Hodgson et al. 2011; Bartholomew et al. 2022), conservative-alignment in SLA might shift when resources become scarcer.

The intermediate, not the lowland, progeny maximized Hill diversity in *S. johorensis*. Echoing Axelsson et al. (2022): as some tree species might host richer invertebrate communities than others, so might certain progeny within species. Accounting for site-effects could provide stronger evidence for or against this conclusion—or, alternatively, produce a more generalizable model. Species distributions are often very localized in the humid tropics (Scheffers et al. 2012), and so should depend significantly on host nativity. And since tropical rainforest insect communities shift along elevation (Beck & Khen 2007; Macedo et al. 2018), factorizing common garden and mother tree parameters can investigate potential interactions causing progenic influences on community structure to vary along environmental gradients. When biocoenoses are as diverse and localized as the communities of the humid tropics, it is not unreasonable to assume influences from host trees to be local as well. These hypotheses are next in line. However, again, sampling has to expand.

Conclusions

In a real forest, where dipterocarps were managed with liberation treatments, mother tree elevation explained up to 13 percent of the variance in physical and phytochemical stem and leaf trait expression of less-than four-year-old planted seedlings. Although explained variance was inconsistent between species, these trait expressions infer significant intraspecific differences in height and diameter growth, total and specific leaf areas, and foliar chlorophyll, P and K contents. Mother tree soil quality was the favored genetic predictor for estimating foliar K content, in all species. Mother tree elevation produced a stronger response in *S. argentifolia* height growth than soil quality. In *P. tomentella*'s total leaf area, it was opposite. There were, also, some other noteworthy – though lesser – model favors (see *Results* and *Discussion*). Elevation contra soil dominance on trait expression seems to, either, be trait-specific, or perhaps more likely, require further seedling development to realize.

In *S. johorensis*, foliar community structure depended on seedling progeny. One in particular hosted many more unique species than the others. And common-species evenness increased in the progeny from intermediate elevations. After accounting for environmental influence, *S. johorensis* mother tree elevation was able to explain 12 percent of the variance in alpha diversity and 9 percent in beta diversity within progeny. No other dipterocarp species produced these kinds of responses, but *S. argentifolia*'s trait-constrained multivariate community median locations varied significantly. And their separation was significantly influenced by specific leaf area, foliar N, and height growth, and followed weak but significant mother tree elevation and soil quality gradients. Specific leaf area was additionally a significant community constraint in *S. fallax* and *S. johorensis*. Total leaf area in *P. tomentella* and *S. johorensis*.

These findings are significant for any kind of management of Bornean dipterocarp forests, as progeny selection may significantly increase forest growth and resilience, and impact extended community structure. By framing population differentiation through functional ecology, trade-offs between ends – e.g. of increased profitability or ecological restoration – can be identified and incorporated into genetic management. Additional insight into dipterocarp genetics and ecology likely will improve foundations for conservation efforts and the sustainable management of dipterocarp forests, which are under threat from wefts of degrading processes.

Epilogue

Funding and partner briefs

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INIKEA, with which the infrastructure for this work was affiliated, is led and sponsored by a collaboration between Innoprise Plantations Berhad (Innoprise) and IKEA Group (IKEA), and attached to research conducted by staff at Universiti Malaysia Sabah and The Swedish University of Agricultural Sciences (SLU). INIKEA staff oversaw the logistics of identifying mother trees, collecting their fruits, common garden establishment and upkeep, providing progenic baseline data, and assisting in field work for this thesis.

Innoprise's business primarily revolves around management and cultivation of Sabahan oil palm plantations, as well as the processing of their products (https://innoprise.com.my/). This implies benefiting short-term from deforestation by oil palm conversion. Additionally, Innoprise has been involved with controversies regarding unfulfilled management plan pledges. Such and similar practices are still common in contemporary Sabahan land-use (Ng et al. 2022).

IKEA is a global furniture designer, producer, and retailer, which relies on the exploitation of natural resources, such as forests for wood and pulp (https://www.ikea.com/). The vast majority of the wood in IKEA's products are certified by various Forest Stewardship Council (FSC) standards, which the company relies on for their sustainability marketing. FSC, however, has continuously failed to incur behavior past the "irresponsible" status-quos of forest management, as the organization itself envisions it, in both Malaysia (Ng et al. 2022) and Sweden (Villalobos et al. 2018).

Conflicting interests

Save the logistic partnership through INIKEA, I acknowledge no explicit association – whether social, cultural, nor economic –, with Innoprise nor IKEA. However, as I wish for well-being and employment of all INIKEA staff, and broadly the prosperity of Luasong and its inhabitants, I make myself implicit in the validation of their employers' business models. Without Innoprise and IKEA, the people of Luasong would be worse off. I do not wish they were. In fact, I want the opposite. And so – neither socially nor economically – I cannot distance myself from these companies and their actions. Since I wish for the well-being of all *people* involved, my interests are implicitly in conflict with the outcome of SLU's and INIKEA's collaborative work. I have done my best to dissociate my analyses from these interests and hope the reader will forgive any, retrospectively determined, objectionable short-comings. This is the limit of my independence.

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Although I felt completely at home in Luasong, the glimpses of Sweden provided to me by my family did make my stay easier. I am sure my trip was probably the most difficult for my mom.

In the epilogue of my B.Sc. thesis I made the unfortunate prediction that Umut Arslan might finish their statistics degree. They did not. Nevertheless, during the writing of this work, they provided me with constant statistical stimuli and made meaningful suggestions. You are the reason I learned random forest modeling and eventually decided to use it for analysis. And many of the statistical tools and concepts that come my way were either your suggestions or spawned out of your remarks. I am trained to solve ecological problems, and am susceptible to any solutions proposed by statistically minded people. Because even when you lack confidence, as a virtue of your field, you have inferential insight into virtually all of contemporary research. As I claimed two years ago, you should not underestimate yourself.

Felix Ecker consistently provided reliable feedback on statistical questions and ideas. Jörgen Sjögren gave useful comments on flower traits and briefly helped me interpret Ashton (2004).

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∞

Time passes. Carolina’s memory has shrunk but now screams in bright red—a burning dot in my forehead. It enters my skull and lodges itself in white matter fold. An inconsolable itch that worsens as the locus of my mind approaches. The singularity does not move. Only slowly as the tissue clasping it melts and then re-hardens. She has become an uninvited, self-important guest I could not evict if I had the will. My mind endures by the whims her mercy.

Strength is not having the courage to fight for justice, but to flourish while doing so. And effortlessly imbuing me with a sliver of yours made, to me, every virtue inevitable. Infinite purpose brefly eclipsing vapid expanse; a self-nested love for life in spite of itself. Then the world lost you, and mine its sympathy.

Mist

A mist rolls through the hills in Luasong at night.

It enters every crevice;

It rests on the surface of a mango fruit,
it coats rusty sheet metal roofs and
the lips of snoring stray dogs.
It saturates the retina of a black hornbill,
and the inside of a ginger's corolla.

The dew fattens, until it cannot bear it;

It collapses into itself and
splashes the ochre litter.
A tractor millipede flinches into a curl.
It is snatched by the hornbill,
who feeds its chicks.

The commotion rattles the dogs.
They howl in synchrony,
and the whole town is awake.

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Ringkasan sains popular

Pembiakbakaan pokok adalah alat yang berkuasa untuk semua pengurus hutan, sama ada untuk tujuan komersial atau pemulihan ekologi. Melalui pembiakbakaan terkawal, ciri-ciri tumbuhan tertentu – seperti pertumbuhan atau ketahanan kemarau – boleh dipertingkatkan untuk memaksimumkan impak pengurusan. Ia bukan sahaja penting untuk membangunkan baka genetik asli yang boleh bersaing secara komersial dengan kaedah penggunaan tanah alternatif, tetapi juga untuk menyesuaikan pokok kepada perubahan iklim yang diramalkan. Memandangkan pembiakbakaan pokok bergantung kepada variasi genetik, mengekalkan kepelbagaiannya adalah insentif. Spesies dipterokarpa dianggap sebagai asas bagi hutan Borneo, oleh itu, menumpukan kepada pengurusan genetiknya mungkin akan memaksimumkan usaha pemuliharaan hutan hujan.

Dalam kajian ini, saya menyiasat pertumbuhan fizikal dan kimia daun pada anak pokok dipterokarpa yang ditanam. Terdapat perbezaan yang ketara antara baka genetik, dan perbezaan tersebut mengikut aras ketinggian dan kecerunan tanah. Anak pokok yang ibunya berasal dari persekitaran tanah rendah yang subur umumnya tumbuh lebih cepat, dan begitu juga sebaliknya. Selain itu, saya menginventori kelimpahan spesies serangga pada anak pokok tersebut. Dalam salah satu spesies dipterokarpa, ketinggian pokok ibu sahaja mampu menyumbang sebanyak 12 peratus daripada variasi kekayaan serangga – dalam persekitaran hutan yang realistik. Ini bermakna, komuniti serangga bertindak balas secara khusus terhadap genetik dipterokarpa. Ciri-ciri fizikal dan kimia anak pokok secara keseluruhan tidak mempengaruhi komuniti serangga dengan jelas, namun keluasan daun dan pertumbuhan ketinggian mengubahnya secara konsisten. Oleh itu, terdapat hubungan yang jelas, keadaan iklim pokok ibu kepada pembangunan anak pokok serta kepada struktur komuniti serangga.

Pembiakbakaan dan penanaman tumbuhan secara terkawal bukan sahaja boleh memberikan manfaat dalam hasil komersial, tetapi juga kekayaan spesies serangga. Malangnya, perkara kedua diabaikan secara global. Berpotensi memudaratkan. Memandangkan ciri-ciri berkaitan pertumbuhan kelihatan mengawal komuniti serangga daun dipterokarpa, pembiakbakaan untuk tujuan memanipulasi kadar pertumbuhan semata-mata mungkin memperkenalkan kesan yang tidak diingini terhadap struktur ekosistem yang lebih luas. Hasil ini bukan sahaja bererti untuk pengurusan hutan dipterokarpa, tetapi untuk pembiakbakaan pokok secara amnya. Para pembiak baka pokok perlu mempertimbangkan pengaruh pemilihan buatan di luar ciri-ciri pokok, dan melaksanakan protokol untuk meminimumkan pemilihan ke arah degradasi biologi yang tidak diingini, seperti pengurangan komuniti serangga lanjutan.

Popular science summary

Tree breeding is a powerful tool for all forest managers, whether for commerce or ecological restoration. Through controlled breeding, certain plant properties – like growth or drought resilience – can be amplified to maximize management impacts. Not only is this important for developing native genetic lines that can commercially compete with alternative land-use methods, but also for adapting trees to predicted climate changes. And since tree breeding depends on a supply of genetic variation, maintaining its diversity would be incentivized. The dipterocarps are considered foundational for Borneo's forests, focusing on managing their genetics might therefore maximize rainforest conservation efforts.

Here, I investigated physical growth and leaf chemistry in planted dipterocarp seedlings. There were considerable differences between genetic lines, and these followed elevational and soil gradients. Seedlings with mothers from fertile lowland environments generally grew faster, and *vice versa*. In addition, I inventoried insect species abundances on these seedlings. In one of the dipterocarps, mother tree elevation, alone, was able to account for 12 percent of the variation in insect richness—in a realistic forest environment. Meaning, insect communities responded specifically to dipterocarp genetics. Seedling physical and chemical properties did not influence insect communities strongly overall, but leaf area and height growth changed them consistently. There is therefore a clear relationship from mother tree climate conditions to seedling development to insect community structure.

Not only might controlled plant breeding and planting provide benefits in commercial yield, but also insect species richness. Unfortunately, the latter is neglected, globally. Potentially detrimentally. Since growth-related properties seem to be regulators of dipterocarp foliar insect communities, breeding them for the sole purpose of manipulating growth rates might introduce unwanted consequences for broader ecosystem structure. Not only are these results significant for dipterocarp forest management, but tree breeding generally. Tree breeders ought to consider the influence of their artificial selection beyond the trees' properties, and implement protocol to minimize selection for unwanted biological degradation, like impoverished extended insect communities.

Appendix 1

Common garden phytosociological structure

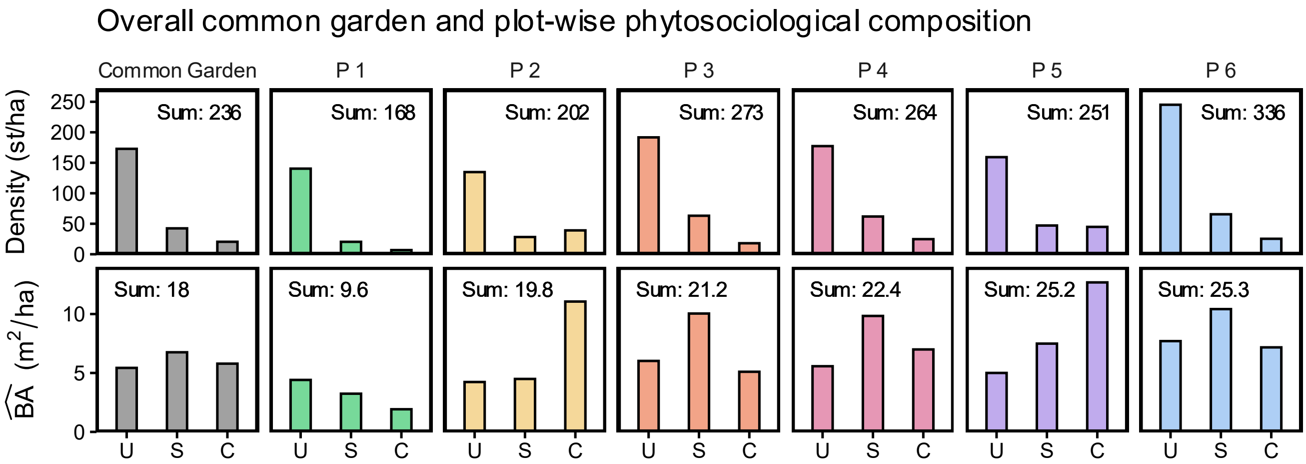


Figure 14. Overall common garden and plot-wise stem and basal area ($\widehat{BA}$) densities over D_{BH}-classes (U = understorey trees [10-30 cm], S = sub-canopy trees [30-60 cm], and C = canopy trees [>60 cm]). Since the trees were categorized by D_{BH} ranges, the basal areas are only approximates ($\widehat{BA}$). And even though stem density should decay exponentially, basal area is likely underestimated since the largest ordinal category (C) lacks an upper limit criterion and trees <10 cm D_{BH} were not counted. Plots ordered by increasing estimated basal area ($\widehat{BA}$).

Appendix 2

Leaf weight convergence and convergence statistics

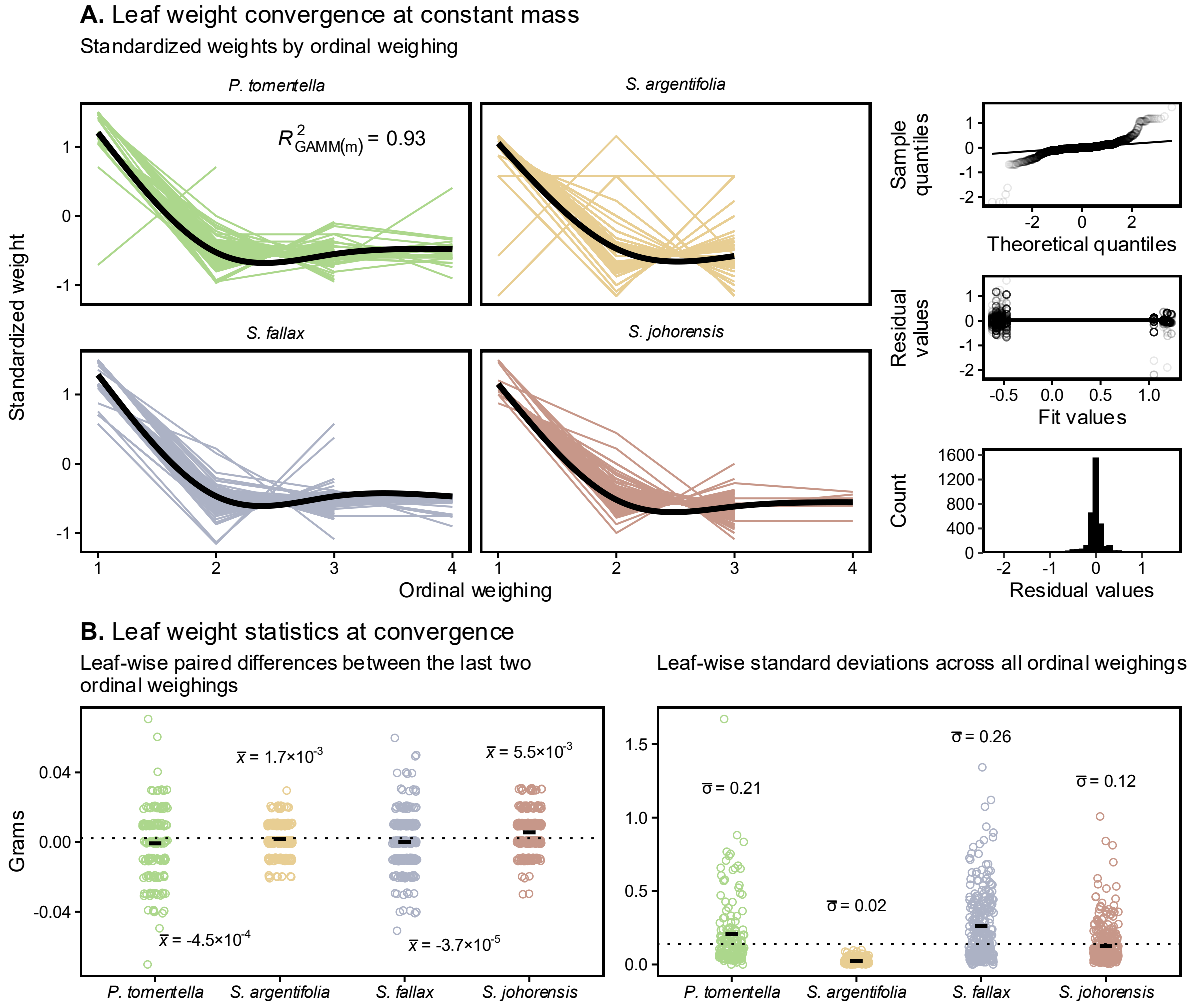


Figure 15. **A.** Convergence of standardized weight by ordinal weighing as a Generalized Additive Mixed Model (GAMM). Smooths and intercepts allowed to vary across species, with leaf identity as the conditional term for random effects to account for repeated weighings (linear groupings). Only fixed effect estimates (black solid lines), and their marginal variance explained shown (Nakagawa & Schielzeth's [2013] $R^2_{GLMM(m)}$ implemented for GAMM). With Q-Q plot, conditional distribution (mean estimated with LOESS), and histogram of residuals. **B.** Species-wise leaf weight differences between the last two ordinal weighings (x) and standard deviations across all ordinal weighings (σ). Species-wise means of differences ($\bar{x}$) and standard deviations ($\bar{\sigma}$) as solid lines, and overall means ($\bar{\bar{x}}$=2.1×10^{-3} and $\bar{\bar{\sigma}}$=0.14) as dotted lines. n_{PT}=153, n_{SA}=318, n_{SF}=267, n_{SJ}=339.

Appendix 3

Validity of leaf morphospecies inventory

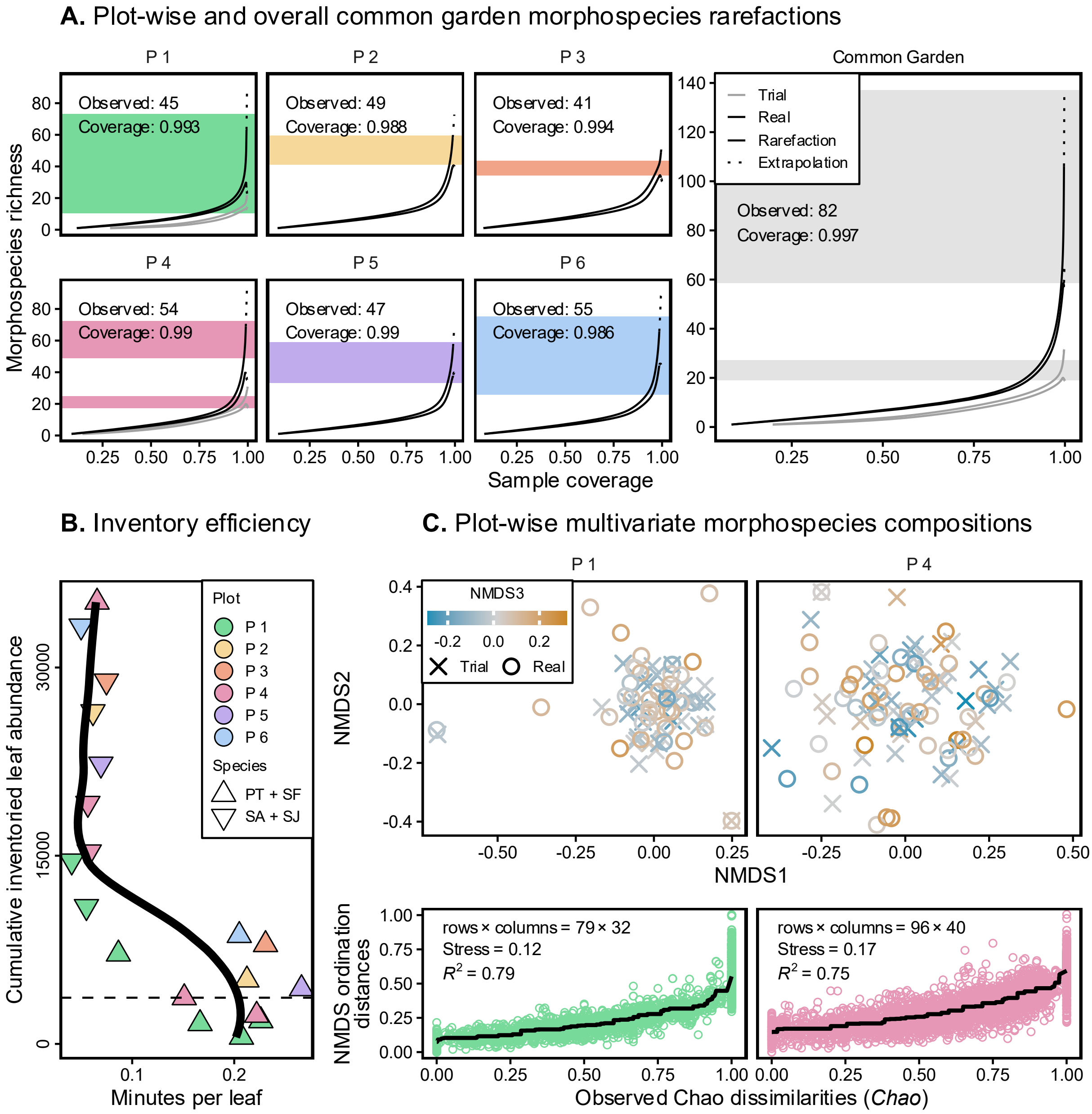


Figure 16. **A.** 95 percent CIs of coverage-based leaf morphospecies richness rarefactions and extrapolations within plots and across the common garden. Colored ribbons are lower halves of asymptote 95 percent CIs. The trial runs found 17 species in P1 with 0.99 coverage and 24 in P 4 with 0.99 coverage, and 25 in the whole common garden with 0.99 coverage. Rarefaction performed with

iNEXT::iNEXT(q = 0, nboot = 200, knots = c(1000, 3000), conf = 0.95) (Hsieh et al. 2024). **B.** Running leaf inventory efficiency as minutes per leaf as a LOESS-function of cumulative inventoried leaf abundance (axes flipped), with the last trial run as a dashed line. Species denotes which dipterocarps were inventoried. **C.** Morphospecies ordinations by NMDS (Kruskal 1964), of real and trial inventory runs, with corresponding Shepard plots and model fit statistics. *Chao*-space centroid location varied significantly between runs in both plots (PERMANOVA; P 1: $\hat{F}_{1,\ 77}$=7.82, $\hat{p}$<0.01; P4: $\hat{F}_{1,\ 94}$=3.89, $\hat{p}$<0.01), dispersion did not. 9999 permutations each. *Chao* produced absolute values (0 or 1) in about 18 percent of the pairs. Morphospecies M1 excluded. NMDS dimensions rotated with PCA, performed with *vegan::metaMDS(distance = "chao", engine = "global", k = 3, maxit = 200, try = 50, trymax = 100, weakties = TRUE)* (Oksanen et al. 2025).

Appendix 4

Model validation, residuals, and convergence

Common frequentist inference and hypothesis tests, such as *t*- and *F*-tests, are relatively robust to violations of assumptions of Gaussian distributions in both variables and modeled residuals. Violations of assumed homoscedasticity, however, may significantly inflate *p*-values and confound effects on means and dispersion (Lumley et al. 2002; Blanca et al. 2017; Knief & Forstmeier 2021). Also, tests for normality frequently, either, lack power or asymmetrically weigh few outliers over the vast majority of data (Lumley et al. 2002). With this in mind, residual assumptions were not tested, but instead investigated visually. And when distributions seemed potentially problematic, skewness and kurtosis were calculated and compared to empirically investigated intervals (Blanca et al. 2017).

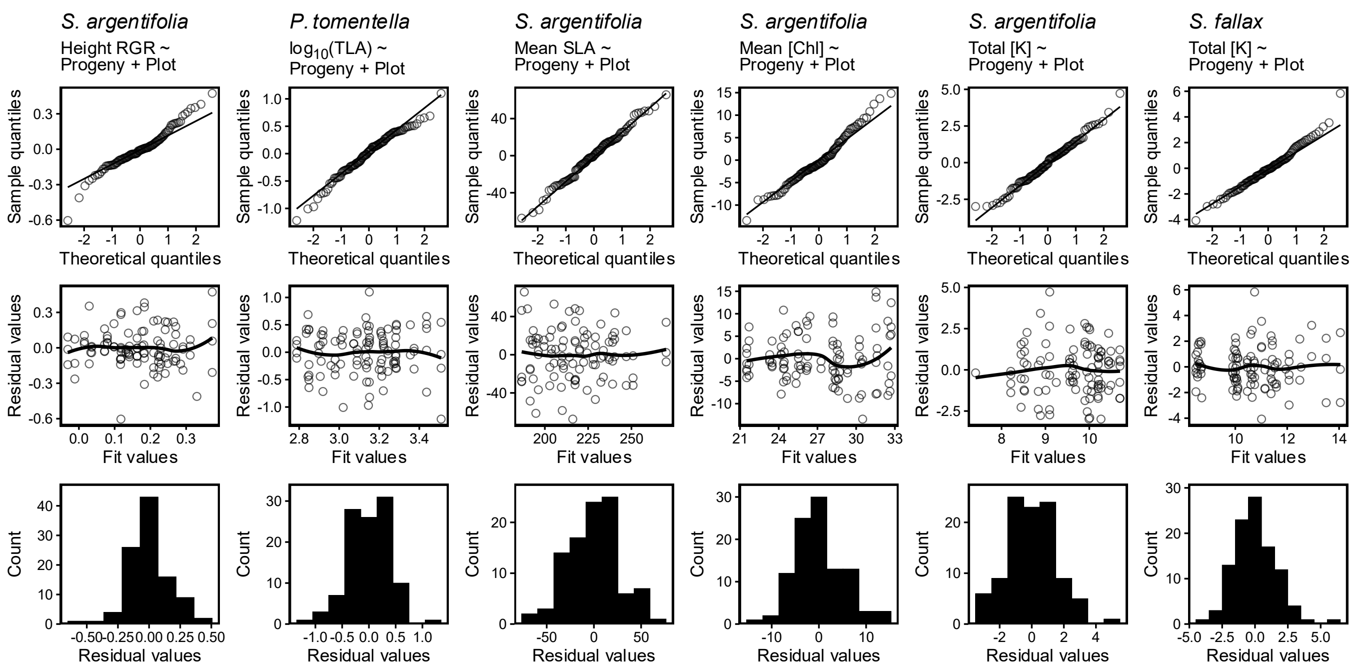


Figure 17. QQ-plots, conditional distributions (means estimated with LOESS), and histograms of residuals from two-way ANOVAs of progeny means of height RGR, $\log_{10}$(total leaf area) (TLA), mean SLA, and mean foliar chlorophyll (Chl) and total foliar K contents of *Shorea argentifolia*, *Parashorea tomentella*, and *S. fallax*.

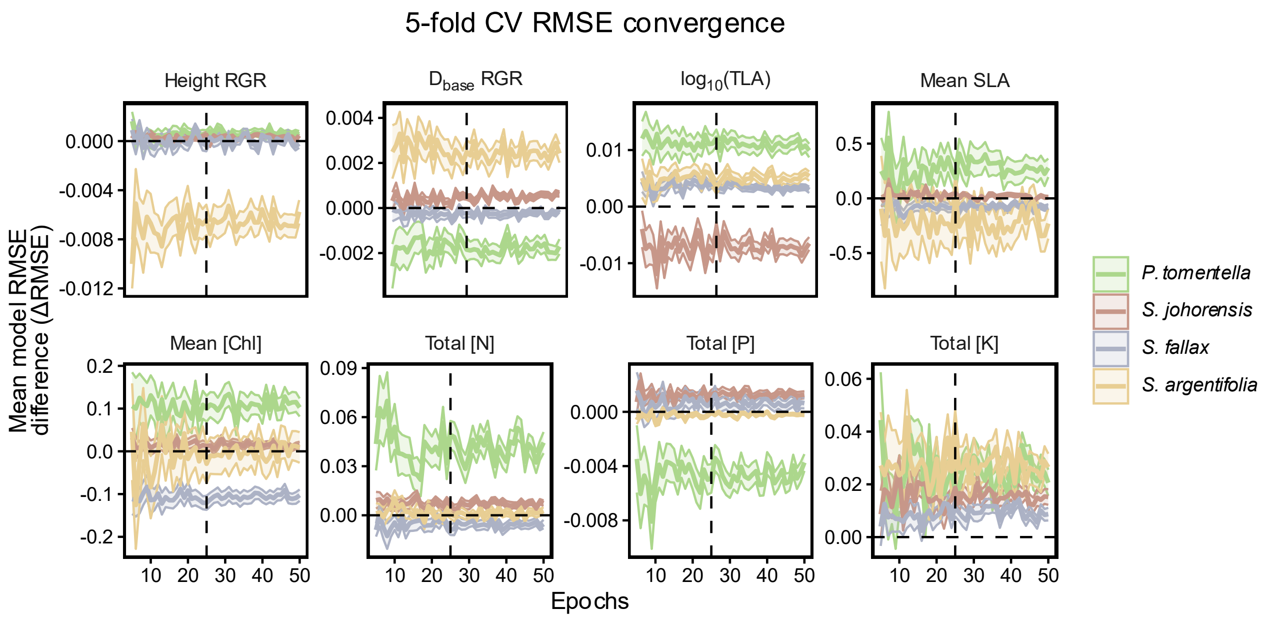


Figure 18. Convergence of the mother tree elevation (Elevation) and soil quality (Soil) models' 5-fold cross-validated mean RMSE differences ± SEs across epochs in height RGR, D_{base} RGR, log_{10}(total leaf area), mean SLA, mean foliar chlorophyll (Chl) content, and total foliar N, P, and K contents for all four dipterocarp species. Dashed black lines highlight favor-threshold ($\Delta RMSE=0$; Elevation is favored when $\Delta RMSE<0$ and Soil when $\Delta RMSE>0$) and the selected level for comparison (epochs=25).

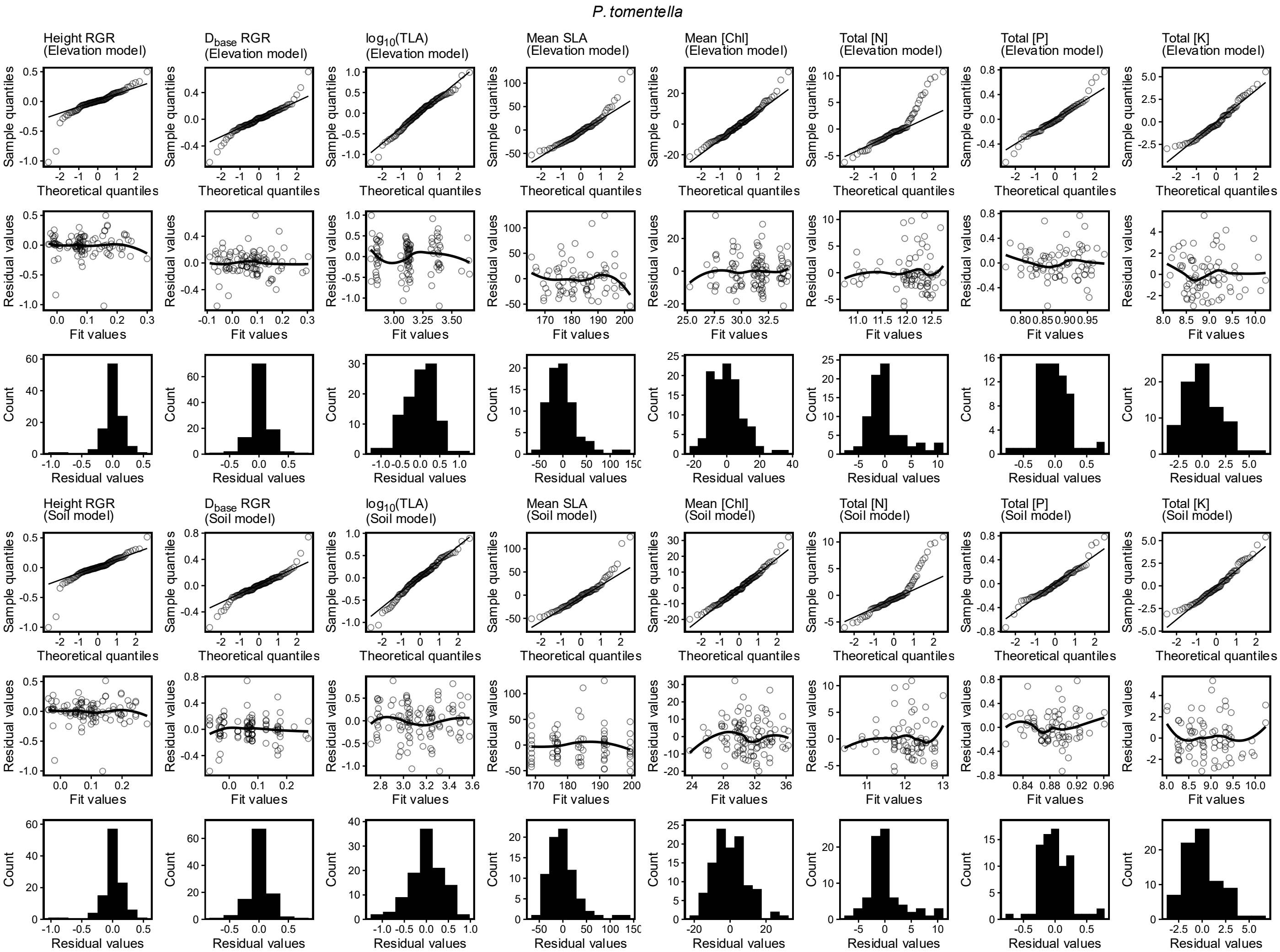


Figure 19. QQ-plots, conditional distributions (means estimated with LOESS), and histograms of residuals from Generalized Linear Models (GLMs) of height RGR, D_{base} RGR, $\log_{10}$(total leaf area), mean SLA, mean foliar chlorophyll (Chl) content, and total foliar N, P, and K contents as functions of mother tree elevation (Elevation) or soil quality (Soil), CII, and $\widehat{BA}$, for *Parashorea tomentella*.

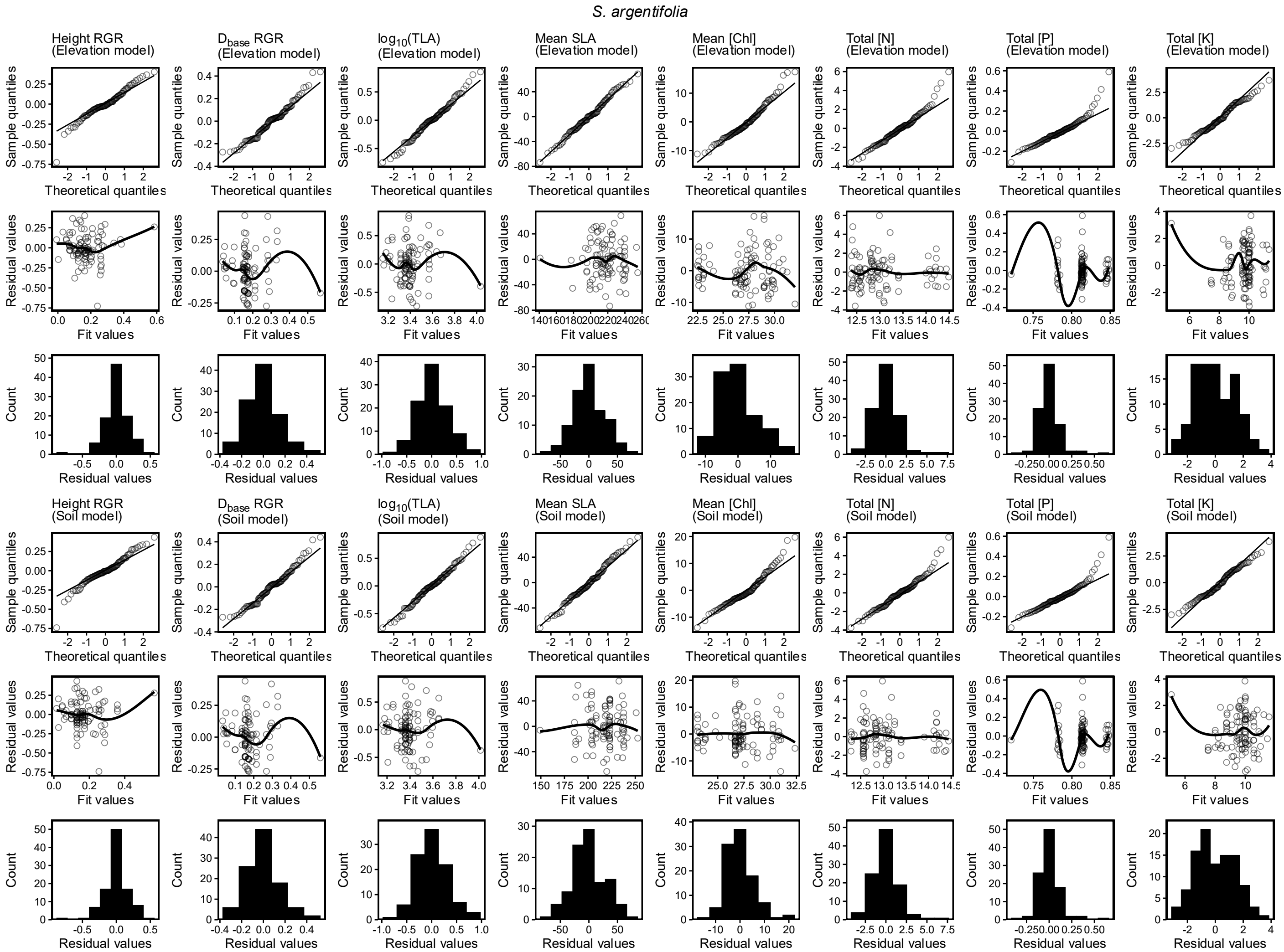


Figure 20. QQ-plots, conditional distributions (means estimated with LOESS), and histograms of residuals from Generalized Linear Models (GLMs) of height RGR, D_{base} RGR, log_{10}(total leaf area), mean SLA, mean foliar chlorophyll (Chl) content, and total foliar N, P, and K contents as functions of mother tree elevation (Elevation) or soil quality (Soil), CII, and $\widehat{BA}$, for *Shorea argentifolia*.

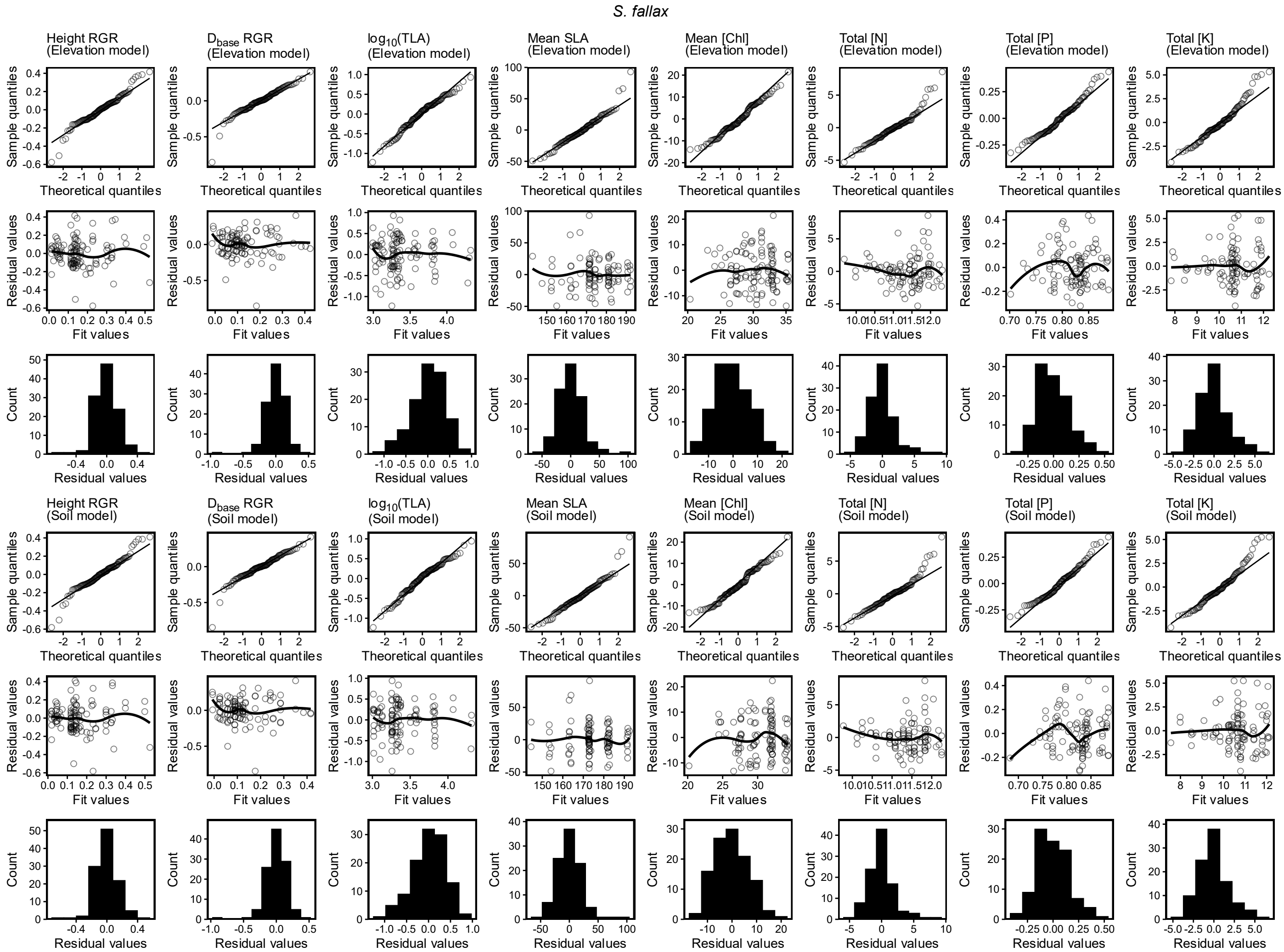


Figure 21. QQ-plots, conditional distributions (means estimated with LOESS), and histograms of residuals from Generalized Linear Models (GLMs) of height RGR, D_{base} RGR, log_{10}(total leaf area), mean SLA, mean foliar chlorophyll (Chl) content, and total foliar N, P, and K contents as functions of mother tree elevation (Elevation) or soil quality (Soil), CII, and $\widehat{\text{BA}}$, for *Shorea fallax*.

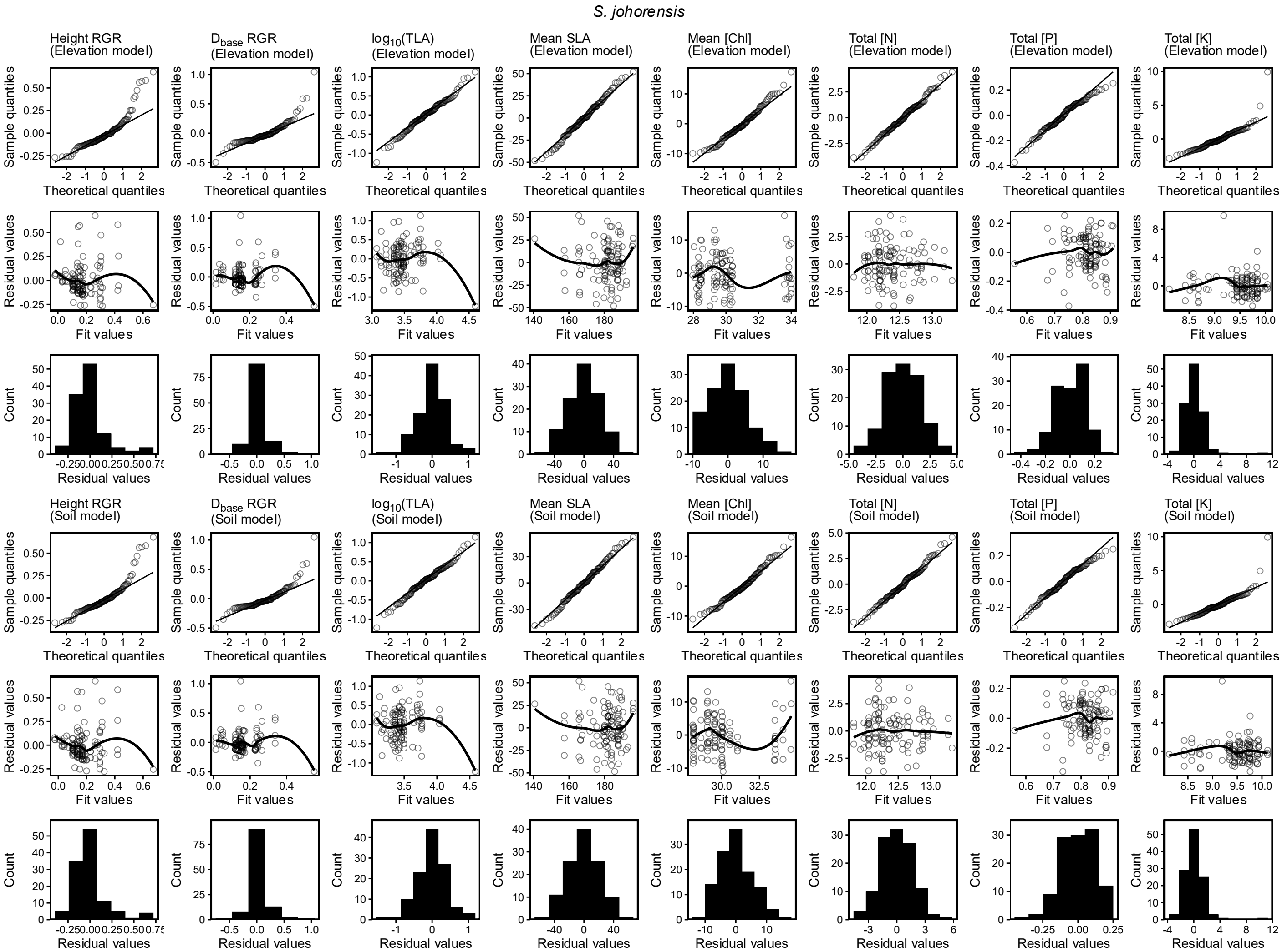


Figure 22. QQ-plots, conditional distributions (means estimated with LOESS), and histograms of residuals from Generalized Linear Models (GLMs) of height RGR, D_{base} RGR, log_{10}(total leaf area), mean SLA, mean foliar chlorophyll (Chl) content, and total foliar N, P, and K contents as functions of mother tree elevation (Elevation) or soil quality (Soil), CII, and $\widehat{BA}$, for *Shorea johorensis*.

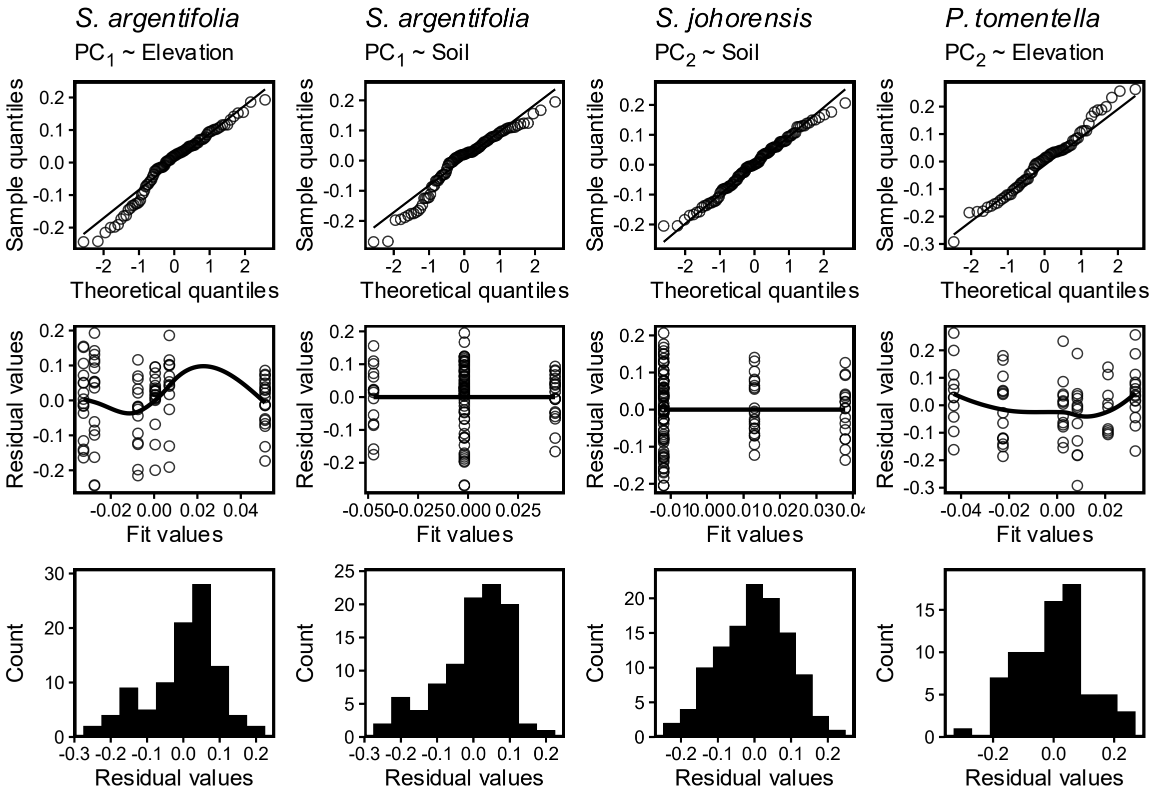


Figure 23. QQ-plots, conditional distributions (means estimated with LOESS and GLM), and histograms of residuals from Generalized Linear Models (GLMs) of principal components (PCs) 1 and 2 of Euclidean seedling trait-space (of height RGR, D_{base} RGR, $\log_{10}$[total leaf area], mean SLA, mean foliar chlorophyll content, and total foliar N, P, and K contents) as functions of mother tree elevation (Elevation) and soil quality (Soil) for *Shorea argentifolia*, *S. johorensis*, and *Parashorea tomentella*.

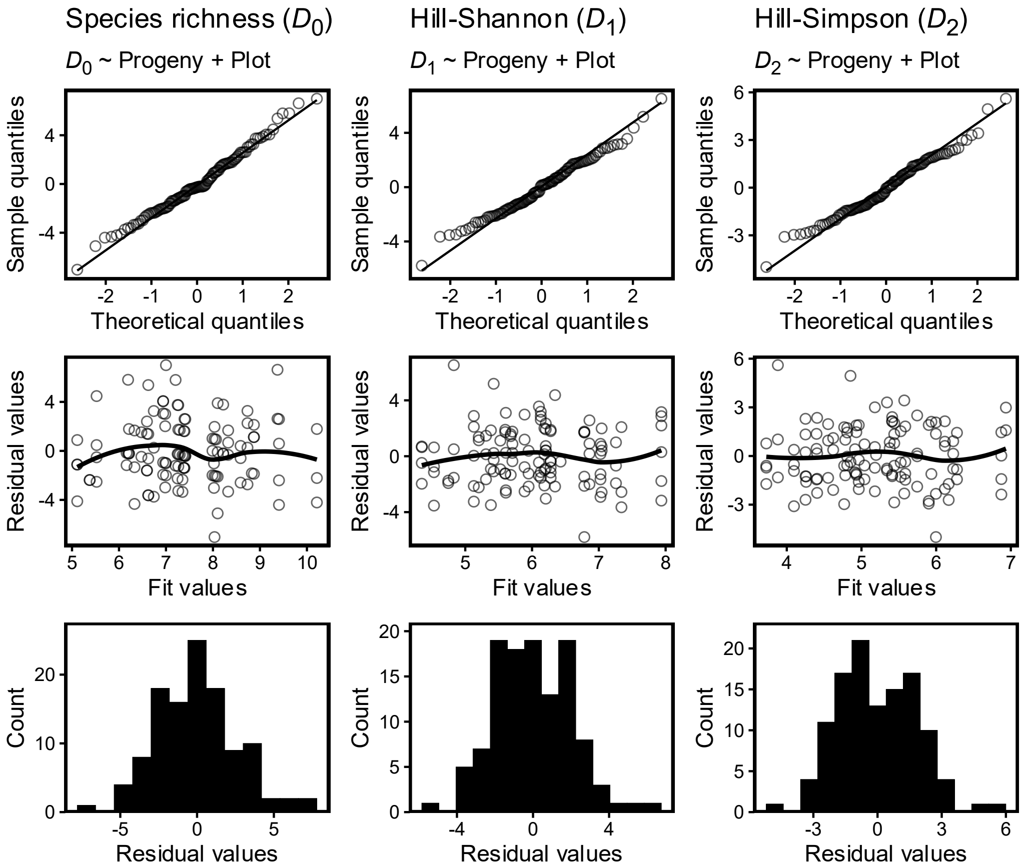


Figure 24. QQ-plots, conditional distributions (means estimated with LOESS), and histograms of residuals from additive two-way ANOVAs of Hill diversity (D_q) as a function of plot and progeny in *Shorea johorensis*.

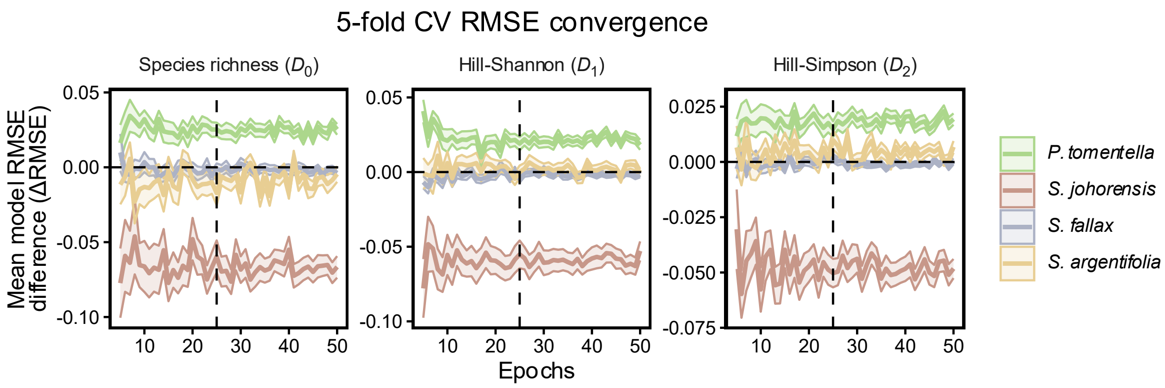


Figure 25. Convergence of the mother tree elevation (Elevation) and soil quality (Soil) models' 5-fold cross-validated mean RMSE differences±SEs across epochs in all three Hill diversities (D_0, D_1, and D_2) for all four dipterocarp species. Dashed black lines highlight favor-threshold (ΔRMSE=0; Elevation is favored when ΔRMSE<0 and Soil when ΔRMSE>0) and the selected level for comparison (epochs=25).

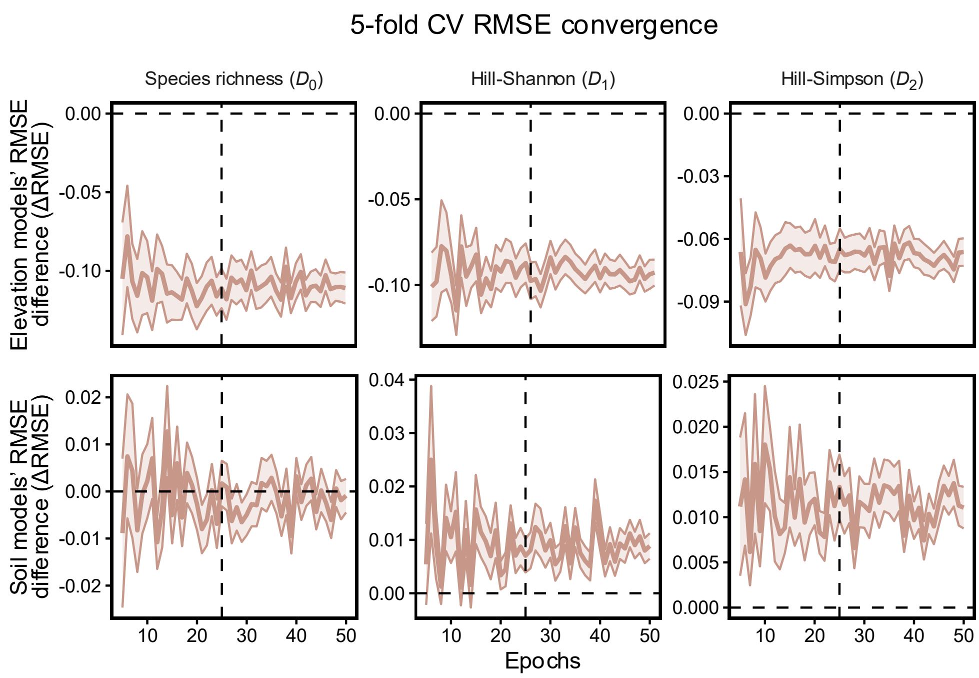


Figure 26. Convergence of the smooth (thin plate spline GAMs) and linear fit (GLMs) Elevation and Soil models' 5-fold cross-validated mean RMSE differences±SEs across epochs in all three Hill diversities (D_0, D_1, and D_2) for *Shorea johorensis*. Dashed black lines highlight favor-threshold (ΔRMSE=0; the smooth is favored when ΔRMSE<0 and the linear fit when ΔRMSE>0) and the selected level for comparison (epochs=25).

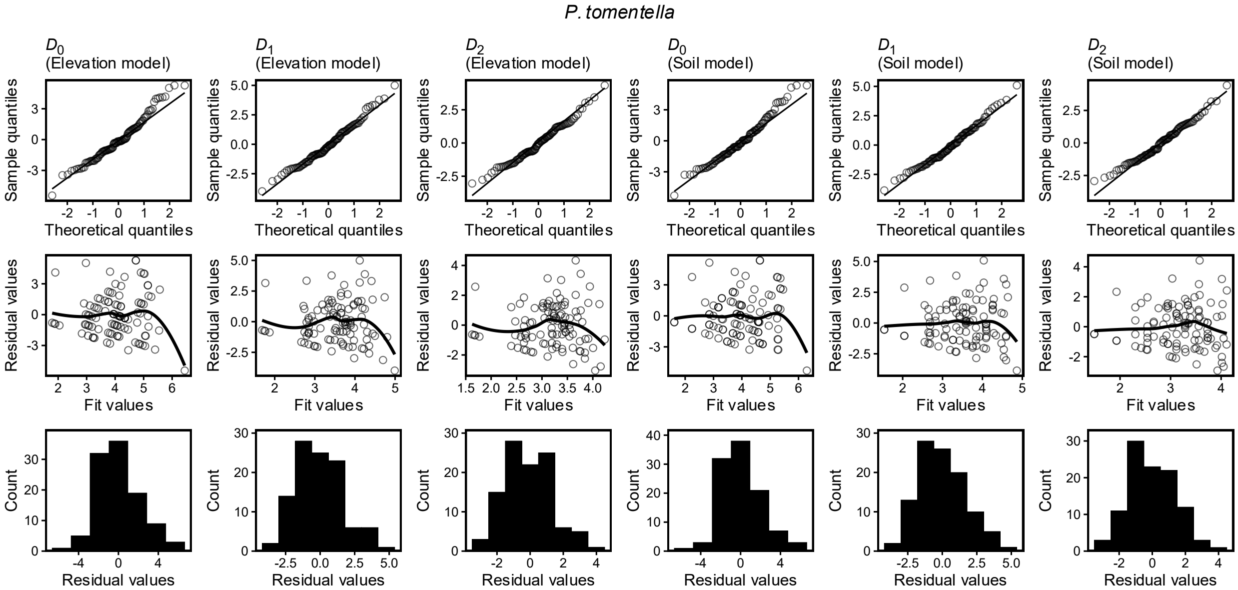


Figure 27. QQ-plots, conditional distributions (means estimated with LOESS), and histograms of residuals from Generalized Additive Models (GAMs) of species richness (D_0), Hill-Shannon (D_1), and Hill-Simpson (D_2) as functions of mother tree elevation (Elevation), soil quality (Soil), CII, and $\widehat{\mathrm{BA}}$, in *Parashorea tomentella*.

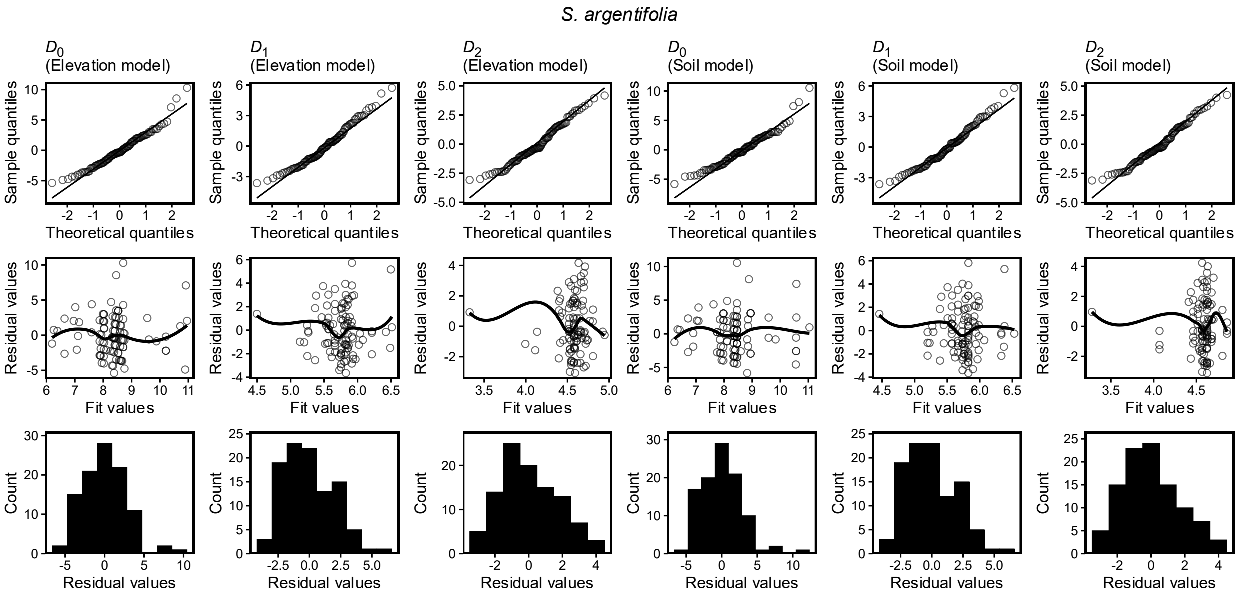


Figure 28. QQ-plots, conditional distributions (means estimated with LOESS), and histograms of residuals from Generalized Additive Models (GAMs) of species richness (D_0), Hill-Shannon (D_1), and Hill-Simpson (D_2) as functions of mother tree elevation (Elevation), soil quality (Soil), CII, and $\widehat{\mathrm{BA}}$, in *Shorea argentifolia*.

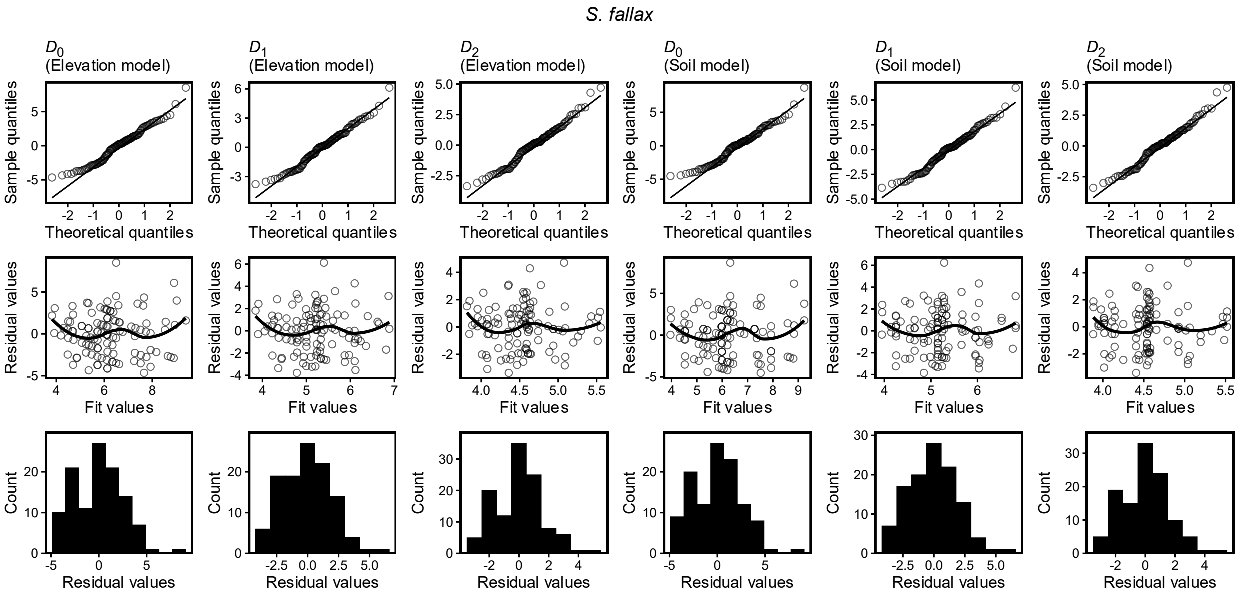


Figure 29. QQ-plots, conditional distributions (means estimated with LOESS), and histograms of residuals from Generalized Linear Models (GLMs) and Generalized Additive Models (GAMs) of species richness (D_0), Hill-Shannon (D_1), and Hill-Simpson (D_2) as functions of mother tree elevation (Elevation), soil quality (Soil), CII, and $\widehat{\mathrm{BA}}$, in *Shorea fallax*.

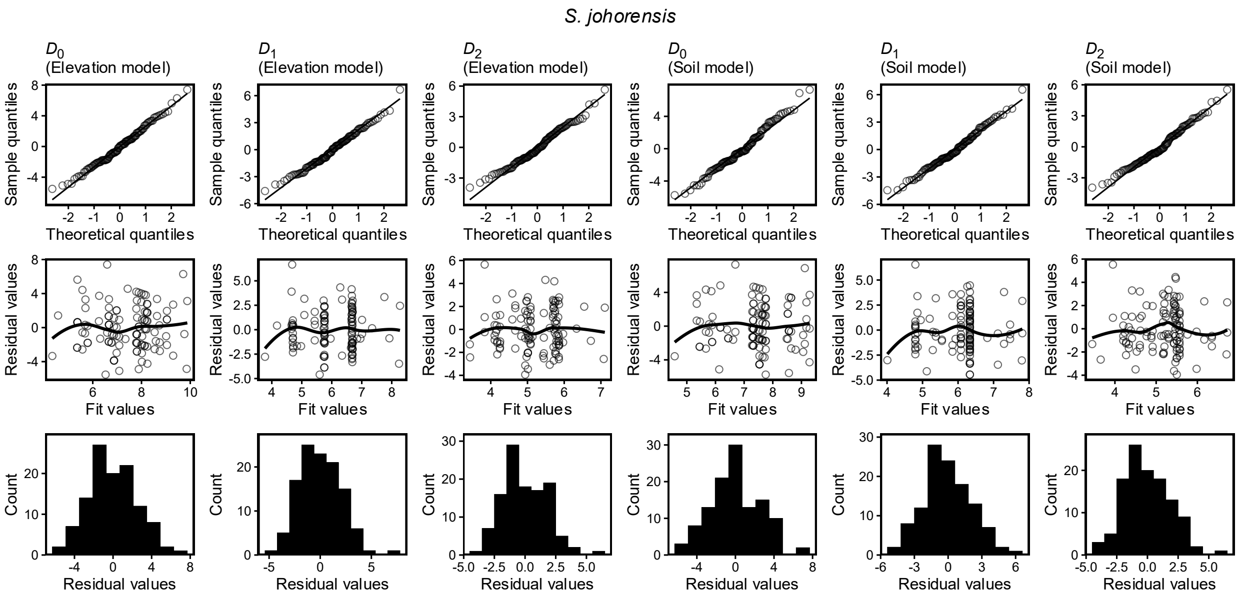


Figure 30. QQ-plots, conditional distributions (means estimated with LOESS), and histograms of residuals from Generalized Additive Models (GAMs) of species richness (D_0), Hill-Shannon (D_1), and Hill-Simpson (D_2) as functions of mother tree elevation (Elevation), soil quality (Soil), CII, and $\widehat{\mathrm{BA}}$, in *Shorea johorensis*.

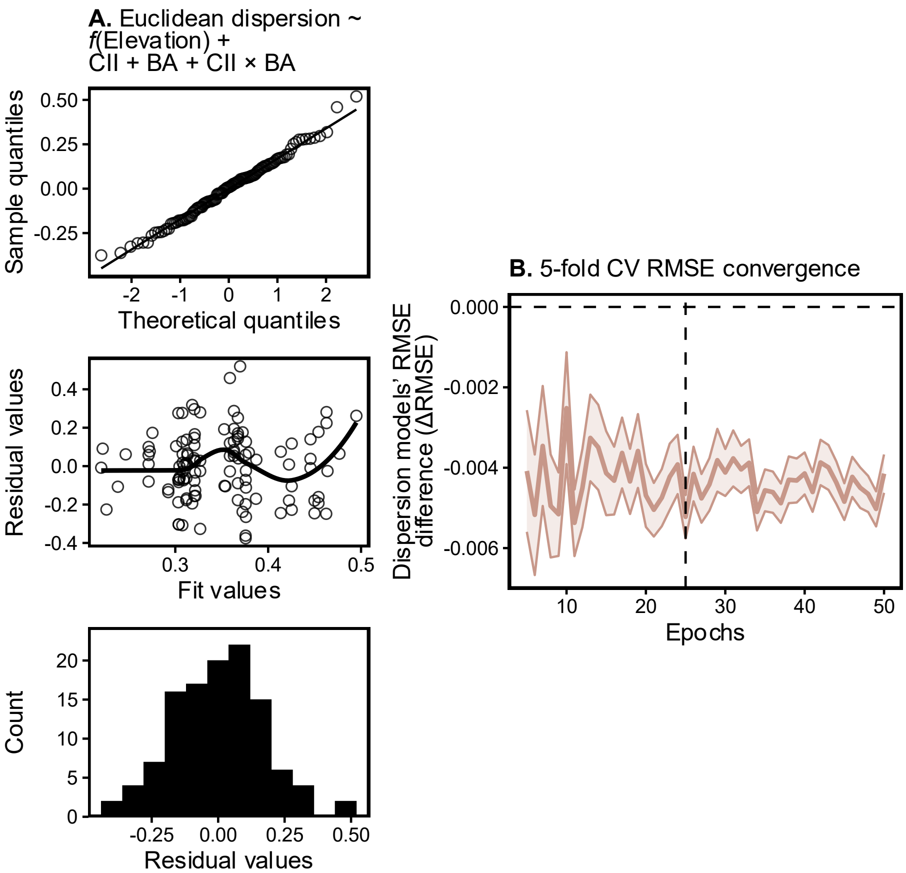


Figure 31. Shorea johorensis Euclidean dispersion (β-diversity) model evaluation. **A.** QQ-plot, conditional distribution (means estimated with LOESS), and histogram of residuals from a Generalized Additive Models (GAMs) of Euclidean dispersion from median locations in leaf morphospecies *Chao*-space as functions of mother tree elevation (Elevation), CII, and $\widehat{\mathrm{BA}}$. **B.** Convergence of the smooth (thin plate spline GAMs) and linear fit (GLM) model's 5-fold cross-validated mean RMSE differences±SEs across epochs. Dashed black lines highlight favor-threshold (ΔRMSE=0; the smooth is favored when ΔRMSE<0 and the linear fit when ΔRMSE>0) and the selected level for comparison (epochs=25).

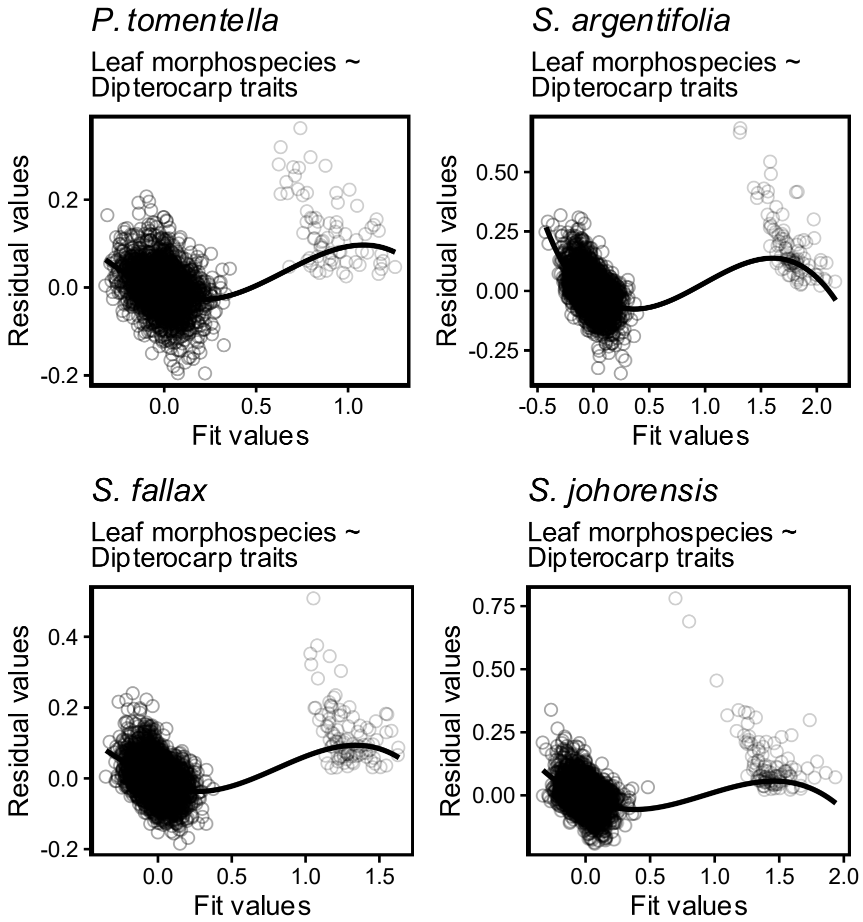


Figure 32. Conditional distributions (means estimated with LOESS) of residuals from Distance-Based Redundancy Analyses (db-RDAs) of dipterocarp seedling trait-constraints on *Chao*-space leaf morphospecies communities for all four dipterocarp species.

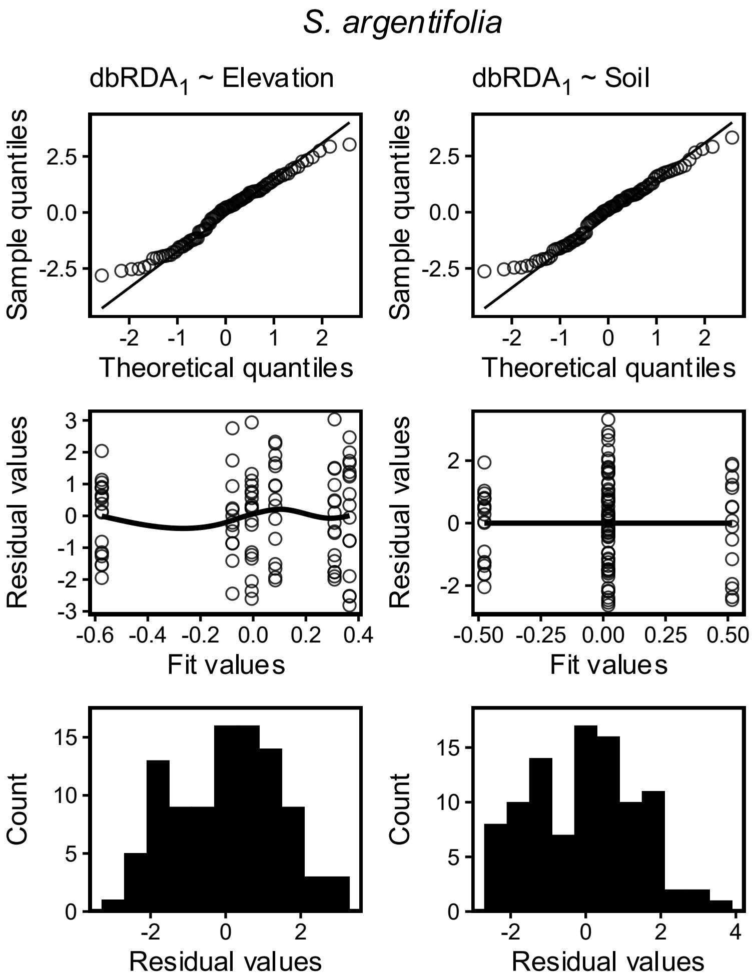


Figure 33. QQ-plots, conditional distributions (means estimated with LOESS), and histograms of residuals from Generalized Linear Models (GLMs) of constrained principal coordinates 1 and 2 ($dbRDA_1$ and $dbRDA_2$) of leaf morphospecies *Chao*-space as functions of mother tree elevation (Elevation) and soil quality (Soil) in *Shorea argentifolia*.

Appendix 5

Seedling trait inventory sheet

Line	Plant No	ID	H	D_base	D_bh	LII	Leaf amount

Line	Plant No	ID	H	D_base	D_bh	LII	Leaf amount

Leaf symptom morphological species inventory sheet

Index	Line	TreeNo	ID	Chl_1	Chl_2	Chl_3	Comments						
M:	M:	M:	M:	M:	M:	M:	M:	M:	M:	M:	M:	M:	M:

Index	Line	TreeNo	ID	Chl_1	Chl_2	Chl_3	Comments						
M:	M:	M:	M:	M:	M:	M:	M:	M:	M:	M:	M:	M:	M:

Index	Line	TreeNo	ID	Chl_1	Chl_2	Chl_3	Comments						
M:	M:	M:	M:	M:	M:	M:	M:	M:	M:	M:	M:	M:	M:

Appendix 6

Mortality

In total, 454 of the 720 inventoried trees (63 percent) were still alive and 265 (37 percent) had died. In P 1, 36 percent of the trees died, 35 percent in P 2, 44 percent in P 3, 25 percent in P 4, 37 percent in P 5, and 45 percent in P 6. Of all *P. tomentella*, 35 percent died, 41 percent of *S. argentifolia*, and 36 percent of both *S. fallax* and *S. johorensis*. Between progeny, 20 to 47 percent of *P. tomentella* died, 30 to 50 percent of *S. argentifolia*, 23 to 53 percent of *S. fallax*, and 30 to 43 percent of *S. johorensis*.

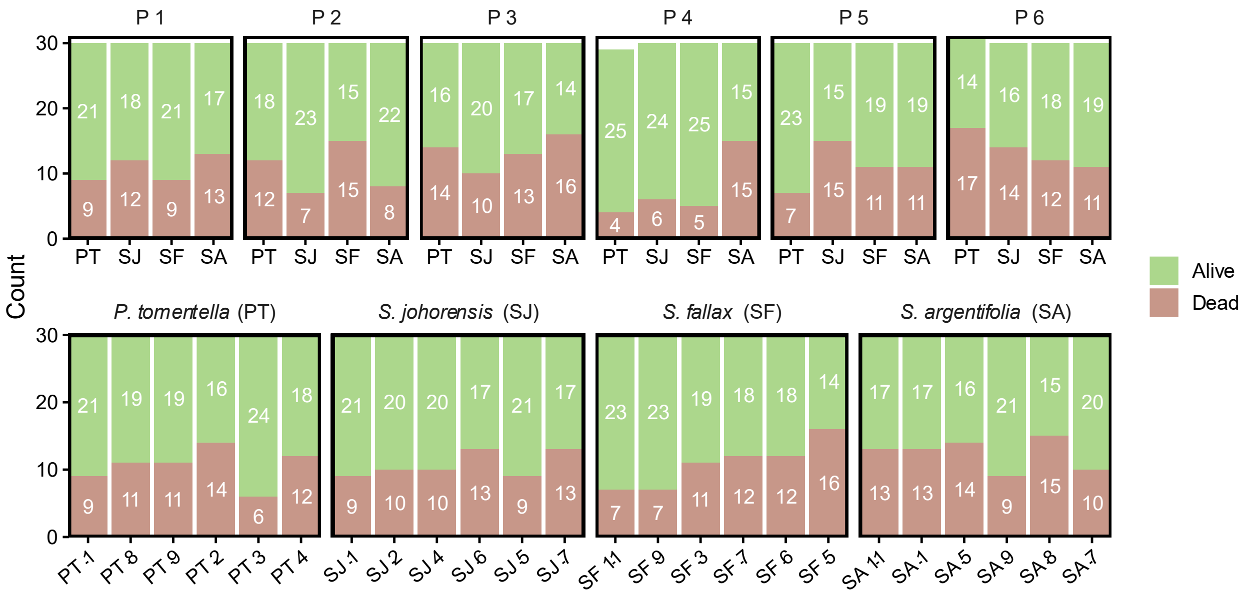


Figure 34. Counts of living and dead individual trees. Progeny sorted, left to right, by increasing mother tree elevation. Plots sorted, left to right, from lowest to highest estimated basal area ($\widehat{BA}$).

Within-species proportion dead trees was modeled as a function of progeny and common garden plot-allocation by two-way ANOVA. Even though mortality seems to increase linearly along mother tree elevation in *S. fallax* (*Figure 34*), there were no significant differences between progeny. Only between plots in *P. tomentella* ($F_{5,25}$=4.56, p<0.01). This is likely due to its low mortality rates in P 4 (*Figure 34*).

Interspecific seedling trait summary

Table 5. Species-wise seedling trait summary.

Species	Trait	Unit	Mean	SD	Sample size
Parashorea tomentella (Symington) Meijer	Leaf abundance	Count	16.30	17.77	108
	Height RGR	-	0.09	0.20	108
	D_{base} RGR	-	0.07	0.19	108
	log_{10}(TLA)	$log_{10}(cm^2)$	3.13	0.44	107
	SLA	cm^2/g	183.63	33.61	76
	Foliar Chl	$\mu mol/m^2$	31.17	9.83	108
	Foliar N	mg/g	12.05	3.48	77
	Foliar P	mg/g	0.88	0.25	77
	Foliar K	mg/g	8.93	1.88	77
Shorea argentifolia Symington	Leaf abundance	Count	165.58	131.08	102
	Height RGR	-	0.17	0.19	102
	D_{base} RGR	-	0.17	0.17	102
	log_{10}(TLA)	$log_{10}(cm^2)$	3.39	0.34	101
	SLA	cm^2/g	217.55	33.07	99
	Foliar Chl	$\mu mol/m^2$	27.19	6.30	102
	Foliar N	mg/g	13.04	1.71	102
	Foliar P	mg/g	0.81	0.13	102
	Foliar K	mg/g	9.60	1.69	102
Shorea fallax Meijer	Leaf abundance	Count	43.75	47.33	114
	Height RGR	-	0.16	0.19	114
	D_{base} RGR	-	0.13	0.19	114
	log_{10}(TLA)	$log_{10}(cm^2)$	3.38	0.49	114
	SLA	cm^2/g	173.74	25.64	102
	Foliar Chl	$\mu mol/m^2$	30.31	7.81	114
	Foliar N	mg/g	11.36	2.25	103
	Foliar P	mg/g	0.82	0.16	103
	Foliar K	mg/g	10.61	2.10	103
Shorea johorensis Foxw.	Leaf abundance	Count	63.47	66.51	115
	Height RGR	-	0.17	0.20	115
	D_{base} RGR	-	0.16	0.20	115
	log_{10}(TLA)	$log_{10}(cm^2)$	3.48	0.46	115
	SLA	cm^2/g	181.00	23.09	115
	Foliar Chl	$\mu mol/m^2$	30.03	5.65	115
	Foliar N	mg/g	12.39	1.68	115
	Foliar P	mg/g	0.81	0.13	115
	Foliar K	mg/g	9.48	1.61	115

Mean height and D_{base} RGR were smallest in *P. tomentella* and largest in *S. argentifolia* and *S. johorensis*. The difference was close to two-fold, though the variances were similar between species. Mean log_{10}(TLA) was smallest in *P.*

tomentella, similar in *S. argentifolia* and *S. fallax*, and largest in *S. johorensis*. Mean SLA, on the other hand, was smallest in *S. fallax*, similar in *P. tomentella* and *S. johorensis*, and largest *S. argentifolia*. The phytochemical traits were roughly similar between all species (*Table 5*).

Interspecific Hill diversity summary

Table 6. Species-wise summary of coverage-based rarefied Hill diversity.

Species	Hill diversity	Coverage	Mean	SD	Sample size
Parashorea tomentella (Symington) Meijer	D_0	0.99	38.00	39.58	106
	D_1	0.99	13.22	6.12	106
	D_2	0.99	7.87	4.84	106
Shorea argentifolia Symington	D_0	0.99	59.00	56.48	102
	D_1	0.99	13.58	2.90	102
	D_2	0.99	9.14	1.92	102
Shorea fallax Meijer	D_0	0.99	49.00	100.36	114
	D_1	0.99	15.54	5.06	114
	D_2	0.99	10.45	3.86	114
Shorea johorensis Foxw.	D_0	0.99	61.00	53.54	115
	D_1	0.99	15.02	4.61	115
	D_2	0.99	9.58	3.30	115

Since leaf abundance constrained morphospecies inventory (see *Leaf symptom morphological species inventory*), these Hill diversity estimates are biased by foliar economic strategy (e.g. area-mass trade-off). Which clearly varied between species (*Table 5*). Interspecific comparison of Hill diversity is not interesting; inference from this data should be limited within species.

Appendix 7

Dipterocarp seedling trait response modeling results

Table 7. Dipterocarp seedling trait response modeling results, with AIC_c, mean and SE of 5-fold cross-validation RMSE, and Random Forest statistics. Significant (p<0.05) effects in bold, close-to-significant (p<0.10) effects in italic. Partial-R^2 as p-R^2.

Model	Species	Response	n	df	AIC_c	$RMSE_{CV}$	SE_{RMSE}	R^2	R^2_{adj}	p-R^2_{Int}	p-R^2_{G}	p-R^2_{CII}	p-R^2_{BA}	p-$R^2_{G\times C}$
Elevation	PT	Height RGR	108	104	-46.525	0.182	0.006	0.140	0.115	0.010	1.57E-03	0.127	0.012	
Elevation	SA	Height RGR	102	97	-64.265	0.175	2.84E-03	0.243	0.212	0.029	0.044	0.126	0.032	0.060
Elevation	SF	Height RGR	113	109	-87.820	0.161	2.72E-03	0.316	0.297	4.24E-03	0.007	0.215	0.023	
Elevation	SJ	Height RGR	115	111	-66.753	0.178	3.64E-03	0.260	0.240	6.57E-04	9.67E-04	0.149	0.114	
Elevation	PT	D_{base} RGR	108	104	-61.856	0.176	3.61E-03	0.188	0.164	0.030	0.018	0.168	0.011	
Elevation	SA	D_{base} RGR	102	98	-88.354	0.156	1.78E-03	0.195	0.171	0.008	4.74E-04	0.174	0.018	
Elevation	SF	D_{base} RGR	113	109	-76.100	0.167	3.78E-03	0.235	0.214	0.013	0.010	0.090	0.063	
Elevation	SJ	D_{base} RGR	115	111	-49.942	0.188	0.005	0.144	0.121	1.89E-04	1.46E-05	0.099	0.035	
Elevation	PT	$\log_{10}$(TLA)	107	103	110.575	0.400	5.85E-03	0.230	0.208	0.421	2.97E-04	0.230	0.003	
Elevation	SA	$\log_{10}$(TLA)	101	97	64.757	0.330	4.32E-03	0.128	0.101	0.641	0.007	0.099	0.012	
Elevation	SF	$\log_{10}$(TLA)	113	108	119.232	0.402	0.005	0.372	0.349	0.308	0.026	0.138	0.071	0.032
Elevation	SJ	$\log_{10}$(TLA)	115	110	121.184	0.413	0.006	0.279	0.253	0.358	0.053	1.98E-03	0.129	0.048

Table 7. (continued)

Model	Species	Response	*n*	*df*	AIC$_c$	RMSE$_{CV}$	SE$_{RMSE}$	R^2	R^2_{adj}	p-R^2_{Int}	p-R^2_{G}	p-R^2_{CII}	p-R^2_{BA}	p-$R^2_{G\times C}$
Elevation	PT	Mean SLA	76	72	753.891	33.080	0.853	0.075	0.036	0.485	0.031	0.048	3.86E-04	
Elevation	SA	Mean SLA	99	94	951.880	29.646	0.315	0.289	0.258	0.374	0.013	0.097	0.027	0.031
Elevation	SF	Mean SLA	101	97	929.702	23.775	0.407	0.171	0.145	0.539	0.031	0.103	2.39E-05	
Elevation	SJ	Mean SLA	115	111	1038.056	21.975	0.258	0.159	0.136	0.541	5.72E-04	0.049	0.100	
Elevation	PT	Mean [Chl]	108	104	805.012	9.798	0.154	0.043	0.016	0.236	3.18E-05	0.037	0.005	
Elevation	SA	Mean [Chl]	102	98	658.461	6.037	0.083	0.147	0.120	0.384	0.128	1.48E-03	0.007	
Elevation	SF	Mean [Chl]	113	109	776.803	7.450	0.081	0.151	0.128	0.365	0.094	0.062	1.33E-04	
Elevation	SJ	Mean [Chl]	115	111	722.108	5.537	0.072	0.101	0.076	0.460	0.001	1.64E-04	0.099	
Elevation	PT	Total [N]	77	73	419.039	3.563	0.062	0.017	-0.023	0.156	2.45E-04	2.32E-03	0.013	
Elevation	SA	Total [N]	102	98	395.042	1.621	0.028	0.119	0.092	0.621	0.008	3.50E-04	0.114	
Elevation	SF	Total [N]	102	98	459.578	2.225	0.042	0.060	0.031	0.211	0.007	0.013	0.040	
Elevation	SJ	Total [N]	115	111	451.668	1.687	0.022	0.033	0.007	0.478	0.011	0.006	0.015	
Elevation	PT	Total [P]	77	73	11.017	0.253	0.005	0.044	0.005	0.322	0.030	0.012	0.006	
Elevation	SA	Total [P]	102	98	-124.078	0.126	2.74E-03	0.022	-0.008	0.505	9.04E-06	0.021	7.06E-05	
Elevation	SF	Total [P]	102	97	-79.355	0.161	2.01E-03	0.073	0.035	0.246	0.011	7.89E-04	0.008	0.022
Elevation	SJ	Total [P]	115	110	-155.394	0.122	1.57E-03	0.193	0.164	0.091	0.037	1.57E-03	0.079	0.028
Elevation	PT	Total [K]	77	73	321.142	1.877	0.031	0.061	0.022	0.445	3.35E-03	0.015	0.051	
Elevation	SA	Total [K]	102	97	370.256	1.515	0.020	0.312	0.283	0.182	0.039	3.23E-03	0.096	0.039
Elevation	SF	Total [K]	102	98	428.057	1.920	0.030	0.202	0.178	0.513	1.02E-03	0.189	0.013	
Elevation	SJ	Total [K]	115	110	437.967	1.544	0.045	0.086	0.053	0.047	0.024	0.013	0.069	0.022

Table 7. (continued)

Model	Species	Response	β_{Int}	SE_{Int}	t_{Int}	p_{Int}	β_{G}	SE_{G}	t_{G}	p_{G}	β_{CII}	SE_{CII}	t_{CII}	p_{CII}
Elevation	PT	Height RGR	-0.127	0.122	-1.044	0.299	1.34E-04	3.33E-04	0.404	0.687	**0.177**	**0.045**	**3.890**	**1.77E-04**
Elevation	SA	Height RGR	*-0.383*	*0.227*	*-1.689*	*0.094*	**1.72E-03**	**8.15E-04**	**2.113**	**0.037**	**0.504**	**0.135**	**3.731**	**3.21E-04**
Elevation	SF	Height RGR	-0.079	0.115	-0.682	0.497	1.09E-04	1.24E-04	0.880	0.381	**0.201**	**0.037**	**5.470**	**2.89E-07**
Elevation	SJ	Height RGR	0.034	0.126	0.270	0.788	5.68E-05	1.73E-04	0.328	0.744	**0.249**	**0.057**	**4.409**	**2.41E-05**
Elevation	PT	D_{base} RGR	*-0.205*	*0.114*	*-1.806*	*0.074*	-4.32E-04	3.10E-04	-1.393	0.167	**0.194**	**0.042**	**4.576**	**1.32E-05**
Elevation	SA	D_{base} RGR	-0.098	0.109	-0.896	0.373	-2.85E-05	1.32E-04	-0.216	0.830	**0.235**	**0.052**	**4.536**	**1.63E-05**
Elevation	SF	D_{base} RGR	0.145	0.122	1.195	0.235	-1.40E-04	1.31E-04	-1.073	0.286	**0.127**	**0.039**	**3.293**	**1.34E-03**
Elevation	SJ	D_{base} RGR	-0.020	0.136	-0.145	0.885	7.51E-06	1.87E-04	0.040	0.968	**0.213**	**0.061**	**3.499**	**6.74E-04**
Elevation	PT	$\log_{10}$(TLA)	**2.217**	**0.256**	**8.659**	**6.97E-14**	1.21E-04	6.92E-04	0.175	0.861	**0.524**	**0.094**	**5.541**	**2.32E-07**
Elevation	SA	$\log_{10}$(TLA)	**3.046**	**0.231**	**13.173**	**2.50E-23**	-2.24E-04	2.81E-04	-0.797	0.428	**0.360**	**0.110**	**3.268**	**1.50E-03**
Elevation	SF	$\log_{10}$(TLA)	**2.635**	**0.380**	**6.935**	**3.12E-10**	*1.81E-03*	*1.07E-03*	*1.687*	*0.095*	**0.801**	**0.193**	**4.152**	**6.60E-05**
Elevation	SJ	$\log_{10}$(TLA)	**4.430**	**0.565**	**7.835**	**3.20E-12**	**-0.006**	**2.28E-03**	**-2.485**	**0.014**	-0.149	0.319	-0.467	0.642
Elevation	PT	Mean SLA	**230.996**	**28.039**	**8.238**	**5.50E-12**	-0.103	0.068	-1.508	0.136	*-18.203*	*9.579*	*-1.900*	*0.061*
Elevation	SA	Mean SLA	**285.114**	**38.011**	**7.501**	**3.51E-11**	-0.153	0.137	-1.121	0.265	**-71.772**	**22.647**	**-3.169**	**2.06E-03**
Elevation	SF	Mean SLA	**194.998**	**18.310**	**10.650**	**5.33E-18**	*0.034*	*0.019*	*1.763*	*0.081*	**-19.029**	**5.691**	**-3.343**	**1.18E-03**
Elevation	SJ	Mean SLA	**176.381**	**15.411**	**11.445**	**1.67E-20**	0.005	0.021	0.252	0.801	**-16.572**	**6.899**	**-2.402**	**0.018**

Table 7. (continued)

Model	Species	Response	β_{Int}	SE_{Int}	t_{Int}	p_{Int}	β_{G}	SE_{G}	t_{G}	p_{G}	β_{CII}	SE_{CII}	t_{CII}	p_{CII}
Elevation	PT	Mean [Chl]	**35.595**	**6.282**	**5.667**	**1.31E-07**	9.86E-04	0.017	0.057	0.954	**-4.687**	**2.342**	**-2.001**	**0.048**
Elevation	SA	Mean [Chl]	**33.083**	**4.233**	**7.815**	**6.28E-12**	**-0.020**	**0.005**	**-3.796**	**0.000**	0.770	2.017	0.382	0.704
Elevation	SF	Mean [Chl]	**41.913**	**5.293**	**7.918**	**2.19E-12**	**-0.019**	**0.006**	**-3.357**	**0.001**	**-4.541**	**1.685**	**-2.694**	**0.008**
Elevation	SJ	Mean [Chl]	**37.907**	**3.902**	**9.716**	**1.62E-16**	-1.39E-03	0.005	-0.261	0.795	-0.236	1.747	-0.135	0.893
Elevation	PT	Total [N]	**10.864**	**2.958**	**3.672**	**4.55E-04**	9.71E-04	0.007	0.134	0.894	-0.415	1.007	-0.412	0.681
Elevation	SA	Total [N]	**14.743**	**1.164**	**12.668**	**2.33E-22**	1.28E-03	1.42E-03	0.902	0.369	0.103	0.555	0.185	0.853
Elevation	SF	Total [N]	**8.896**	**1.740**	**5.112**	**1.58E-06**	-1.55E-03	1.81E-03	-0.854	0.395	0.612	0.543	1.128	0.262
Elevation	SJ	Total [N]	**12.142**	**1.204**	**10.086**	**2.27E-17**	1.83E-03	1.65E-03	1.107	0.271	0.438	0.539	0.812	0.418
Elevation	PT	Total [P]	**1.231**	**0.209**	**5.886**	**1.12E-07**	-7.70E-04	5.13E-04	-1.501	0.138	-0.068	0.071	-0.961	0.340
Elevation	SA	Total [P]	**0.914**	**0.091**	**10.004**	**1.19E-16**	-3.31E-06	1.11E-04	-0.030	0.976	-0.063	0.044	-1.455	0.149
Elevation	SF	Total [P]	**0.894**	**0.159**	**5.625**	**1.79E-07**	4.57E-04	4.44E-04	1.030	0.306	0.022	0.079	0.277	0.783
Elevation	SJ	Total [P]	**0.565**	**0.170**	**3.325**	**1.20E-03**	**1.40E-03**	**6.85E-04**	**2.047**	**0.043**	0.040	0.096	0.416	0.678
Elevation	PT	Total [K]	**11.982**	**1.567**	**7.648**	**6.43E-11**	-1.90E-03	3.84E-03	-0.496	0.622	-0.568	0.533	-1.066	0.290
Elevation	SA	Total [K]	**8.853**	**1.907**	**4.641**	**1.09E-05**	**0.014**	**0.007**	**1.989**	**4.95E-02**	-0.638	1.137	-0.561	0.576
Elevation	SF	Total [K]	**15.139**	**1.491**	**10.153**	**5.65E-17**	-4.91E-04	1.55E-03	-0.316	0.753	**-2.224**	**0.465**	**-4.784**	**6.08E-06**
Elevation	SJ	Total [K]	**5.193**	**2.242**	**2.316**	**0.022**	0.015	0.009	1.650	0.102	1.495	1.265	1.182	0.240

Table 7. (continued)

Model	Species	Response	$\beta_{G\times C}$	$SE_{G\times C}$	$t_{G\times C}$	$p_{G\times C}$	β_{BA}	SE_{BA}	t_{BA}	p_{BA}	δInc-MSE_G	δInc-MSE_{CII}	δInc-MSE_{BA}	RF pseudo-R^2
Elevation	PT	Height RGR	-3.81E-03	3.32E-03	-1.145	0.255					0.056	0.166	0.101	0.145
Elevation	SA	Height RGR	*-0.006*	*3.20E-03*	*-1.803*	*0.074*	**-1.40E-03**	**5.59E-04**	**-2.497**	**0.014**	0.115	0.077	0.021	0.076
Elevation	SF	Height RGR	-0.005	3.08E-03	-1.586	0.116					-0.106	0.265	0.077	0.123
Elevation	SJ	Height RGR	**-0.012**	**3.27E-03**	**-3.783**	**2.52E-04**					-0.007	0.245	0.218	0.215
Elevation	PT	D_{base} RGR	3.29E-03	3.10E-03	1.063	0.290					-0.010	0.273	0.093	0.106
Elevation	SA	D_{base} RGR	-3.75E-03	2.80E-03	-1.340	0.183					-0.013	0.291	0.093	0.168
Elevation	SF	D_{base} RGR	**-0.009**	**3.24E-03**	**-2.708**	**0.008**					-0.096	0.135	0.144	0.074
Elevation	SJ	D_{base} RGR	**-0.007**	**3.51E-03**	**-2.017**	**0.046**					-0.029	0.263	0.148	0.143
Elevation	PT	$\log_{10}$(TLA)	4.17E-03	0.007	0.593	0.555					0.047	0.345	0.044	0.208
Elevation	SA	$\log_{10}$(TLA)	-0.007	0.006	-1.097	0.275					0.054	0.188	0.124	0.098
Elevation	SF	$\log_{10}$(TLA)	**-0.022**	**0.008**	**-2.865**	**0.005**	*-1.30E-03*	*6.89E-04*	*-1.893*	*0.061*	-0.096	0.326	0.186	0.199
Elevation	SJ	$\log_{10}$(TLA)	**-0.031**	**0.008**	**-4.032**	**1.02E-04**	**3.46E-03**	**1.48E-03**	**2.346**	**0.021**	0.060	0.340	0.240	0.239
Elevation	PT	Mean SLA	0.126	0.758	0.167	0.868					0.060	0.146	0.053	0.009
Elevation	SA	Mean SLA	0.864	0.539	1.604	0.112	*0.162*	*0.094*	*1.731*	*0.087*	0.200	0.206	0.165	0.220
Elevation	SF	Mean SLA	0.023	0.484	0.048	0.962					0.124	0.127	0.034	0.135
Elevation	SJ	Mean SLA	**1.398**	**0.398**	**3.512**	**6.44E-04**					0.115	0.173	0.268	0.161

Table 7. (continued)

Model	Species	Response	$\beta_{G\times C}$	$SE_{G\times C}$	$t_{G\times C}$	$p_{G\times C}$	β_{BA}	SE_{BA}	t_{BA}	p_{BA}	δInc-MSE_{G}	δInc-MSE_{CII}	δInc-MSE_{BA}	RF pseudo-R^2
Elevation	PT	Mean [Chl]	0.124	0.171	0.725	0.470					-0.105	-0.028	0.129	-0.014
Elevation	SA	Mean [Chl]	-0.092	0.109	-0.843	0.401					0.278	-0.046	-0.037	0.062
Elevation	SF	Mean [Chl]	0.017	0.141	0.120	0.904					0.216	0.152	-0.030	0.009
Elevation	SJ	Mean [Chl]	**-0.353**	**0.101**	**-3.501**	**6.68E-04**					0.040	-0.114	0.227	0.042
Elevation	PT	Total [N]	0.079	0.081	0.974	0.333					-0.017	0.117	0.071	-0.035
Elevation	SA	Total [N]	**-0.106**	**0.030**	**-3.549**	**5.96E-04**					-0.032	0.057	0.218	0.013
Elevation	SF	Total [N]	**0.093**	**0.046**	**2.011**	**0.047**					0.084	0.101	0.102	-0.021
Elevation	SJ	Total [N]	-0.040	0.031	-1.294	0.198					0.010	0.012	0.151	-0.011
Elevation	PT	Total [P]	-3.79E-03	0.006	-0.664	0.509					-0.008	0.042	0.210	0.078
Elevation	SA	Total [P]	-1.95E-04	2.35E-03	-0.083	0.934					-0.062	1.88E-03	0.022	-0.121
Elevation	SF	Total [P]	-2.96E-03	3.28E-03	-0.902	0.369	-4.20E-04	2.82E-04	-1.487	0.140	0.039	0.076	0.304	0.128
Elevation	SJ	Total [P]	**0.007**	**2.28E-03**	**3.074**	**2.66E-03**	*-7.97E-04*	*4.44E-04*	*-1.796*	*0.075*	0.053	8.51E-04	0.235	0.085
Elevation	PT	Total [K]	*-0.084*	*0.043*	*-1.973*	*0.052*					-0.037	0.047	0.119	-0.065
Elevation	SA	Total [K]	**0.087**	**0.027**	**3.210**	**1.80E-03**	*-0.009*	*4.70E-03*	*-1.982*	*5.03E-02*	-0.049	0.322	0.080	0.168
Elevation	SF	Total [K]	-0.045	0.040	-1.133	0.260					0.148	0.226	0.160	0.245
Elevation	SJ	Total [K]	**0.086**	**0.030**	**2.852**	**0.005**	-0.009	0.006	-1.562	0.121	-0.049	-0.065	0.071	-0.059

Table 7. (continued)

Model	Species	Response	n	df	AIC$_c$	RMSE$_{CV}$	SE$_{RMSE}$	R^2	R^2_{adj}	p-R^2_{Int}	p-R^2_{G}	p-R^2_{CII}	p-R^2_{BA}	p-$R^2_{G\times C}$
Soil	PT	Height RGR	108	104	-48.062	0.182	0.006	0.152	0.128	0.018	0.016	0.127	0.011	
Soil	SA	Height RGR	102	98	-57.821	0.182	3.17E-03	0.176	0.150	3.30E-03	0.011	0.108	0.057	
Soil	SF	Height RGR	113	108	-88.259	0.161	2.79E-03	0.332	0.307	0.030	0.030	0.066	0.027	0.025
Soil	SJ	Height RGR	115	111	-67.136	0.178	3.63E-03	0.262	0.242	1.87E-04	0.004	0.152	0.112	
Soil	PT	D_{base} RGR	108	104	-59.860	0.178	3.73E-03	0.173	0.149	0.075	9.66E-07	0.168	0.010	
Soil	SA	D_{base} RGR	102	97	-91.458	0.153	1.73E-03	0.237	0.205	0.049	0.043	0.094	0.016	0.048
Soil	SF	D_{base} RGR	113	109	-75.668	0.167	3.77E-03	0.233	0.211	0.012	0.007	0.094	0.060	
Soil	SJ	D_{base} RGR	115	111	-50.018	0.188	0.005	0.144	0.121	4.88E-04	6.81E-04	0.101	0.035	
Soil	PT	$\log_{10}$(TLA)	107	103	104.796	0.388	0.006	0.271	0.249	0.454	0.053	0.238	0.005	
Soil	SA	$\log_{10}$(TLA)	101	96	63.278	0.326	4.37E-03	0.160	0.125	0.044	0.035	0.069	0.011	0.039
Soil	SF	$\log_{10}$(TLA)	113	108	117.905	0.398	0.005	0.379	0.356	0.045	0.041	0.093	0.065	0.045
Soil	SJ	$\log_{10}$(TLA)	115	111	125.289	0.417	0.006	0.239	0.218	0.530	2.61E-03	0.135	0.098	
Soil	PT	Mean SLA	76	72	753.041	32.895	0.873	0.085	0.047	0.524	0.041	0.038	3.93E-07	
Soil	SA	Mean SLA	99	95	954.331	29.638	0.336	0.254	0.230	0.474	0.081	0.124	0.053	
Soil	SF	Mean SLA	101	97	929.857	23.860	0.406	0.169	0.144	0.425	0.030	0.109	2.12E-04	
Soil	SJ	Mean SLA	115	111	1038.016	21.927	0.255	0.159	0.137	0.545	9.22E-04	0.049	0.100	

Table 7. (continued)

Model	Species	Response	n	df	AIC_c	$RMSE_{CV}$	SE_{RMSE}	R^2	R^2_{adj}	p-R^2_{Int}	p-R^2_{G}	p-R^2_{CII}	p-R^2_{BA}	p-$R^2_{G\times C}$
Soil	PT	Mean [Chl]	108	104	802.126	9.698	0.142	0.068	0.042	0.254	0.026	0.039	0.006	
Soil	SA	Mean [Chl]	102	97	659.971	6.066	0.086	0.153	0.118	0.008	0.014	0.031	0.012	0.029
Soil	SF	Mean [Chl]	113	109	779.931	7.570	0.079	0.128	0.104	0.312	0.068	0.054	1.96E-03	
Soil	SJ	Mean [Chl]	115	111	721.595	5.525	0.070	0.105	0.080	0.445	0.005	6.59E-06	0.096	
Soil	PT	Total [N]	77	73	418.566	3.514	0.061	0.023	-0.017	0.175	0.006	2.90E-03	0.014	
Soil	SA	Total [N]	102	98	394.948	1.621	0.028	0.120	0.093	0.552	0.009	4.51E-04	0.108	
Soil	SF	Total [N]	102	98	460.265	2.234	0.042	0.053	0.024	0.145	0.001	0.016	0.048	
Soil	SJ	Total [N]	115	111	450.694	1.681	0.022	0.041	0.015	0.479	0.019	0.007	0.013	
Soil	PT	Total [P]	77	73	13.336	0.257	0.005	0.015	-0.026	0.301	2.98E-04	0.010	0.006	
Soil	SA	Total [P]	102	98	-124.080	0.126	2.74E-03	0.022	-0.008	0.445	2.44E-05	0.021	7.84E-05	
Soil	SF	Total [P]	102	98	-80.516	0.160	1.98E-03	0.063	0.035	0.377	0.030	0.045	0.005	
Soil	SJ	Total [P]	115	110	-156.643	0.121	1.53E-03	0.202	0.173	0.117	0.037	5.56E-04	0.081	0.027
Soil	PT	Total [K]	77	73	319.832	1.860	0.031	0.077	0.039	0.507	0.020	0.013	0.057	
Soil	SA	Total [K]	102	98	366.785	1.476	0.018	0.320	0.299	0.463	0.051	0.206	0.087	
Soil	SF	Total [K]	102	98	427.107	1.909	0.031	0.209	0.185	0.457	0.010	0.201	0.015	
Soil	SJ	Total [K]	115	110	437.779	1.525	0.045	0.087	0.054	0.062	0.024	0.011	0.069	0.020

Table 7. (continued)

Model	Species	Response	β_{Int}	SE_{Int}	t_{Int}	p_{Int}	β_G	SE_G	t_G	p_G	β_{CII}	SE_{CII}	t_{CII}	p_{CII}
Soil	PT	Height RGR	-0.148	0.107	-1.382	0.170	0.025	0.020	1.287	0.201	**0.175**	**0.045**	**3.890**	**1.77E-04**
Soil	SA	Height RGR	0.081	0.143	0.570	0.570	-0.032	0.031	-1.039	0.301	**0.208**	**0.060**	**3.446**	**8.38E-04**
Soil	SF	Height RGR	*-0.527*	*0.291*	*-1.815*	*0.072*	*0.215*	*0.118*	*1.817*	*0.072*	**0.484**	**0.175**	**2.768**	**0.007**
Soil	SJ	Height RGR	0.018	0.125	0.144	0.886	0.015	0.022	0.691	0.491	**0.252**	**0.056**	**4.456**	**2.01E-05**
Soil	PT	D_{base} RGR	**-0.294**	**0.101**	**-2.905**	**4.49E-03**	1.87E-04	0.019	0.010	0.992	**0.196**	**0.043**	**4.588**	**1.25E-05**
Soil	SA	D_{base} RGR	**-0.811**	**0.361**	**-2.247**	**0.027**	**0.348**	**0.167**	**2.080**	**0.040**	**0.717**	**0.226**	**3.167**	**2.06E-03**
Soil	SF	D_{base} RGR	0.168	0.148	1.135	0.259	-0.031	0.036	-0.855	0.395	**0.130**	**0.039**	**3.368**	**1.05E-03**
Soil	SJ	D_{base} RGR	-0.031	0.135	-0.233	0.816	0.007	0.024	0.275	0.784	**0.214**	**0.061**	**3.525**	**6.16E-04**
Soil	PT	$\log_{10}$(TLA)	**2.050**	**0.222**	**9.253**	**3.39E-15**	**0.097**	**0.040**	**2.397**	**0.018**	**0.521**	**0.092**	**5.667**	**1.33E-07**
Soil	SA	$\log_{10}$(TLA)	**1.622**	**0.773**	**2.097**	**0.039**	*0.665*	*0.359*	*1.852*	*0.067*	**1.295**	**0.485**	**2.672**	**0.009**
Soil	SF	$\log_{10}$(TLA)	**1.629**	**0.723**	**2.252**	**0.026**	**0.629**	**0.294**	**2.138**	**0.035**	**1.447**	**0.435**	**3.324**	**1.21E-03**
Soil	SJ	$\log_{10}$(TLA)	**3.229**	**0.289**	**11.177**	**6.90E-20**	-0.028	0.052	-0.539	0.591	**0.544**	**0.130**	**4.171**	**6.04E-05**
Soil	PT	Mean SLA	**222.738**	**25.043**	**8.894**	**3.29E-13**	**-7.298**	**4.139**	**-1.763**	**0.082**	*-16.060*	*9.549*	*-1.682*	*0.097*
Soil	SA	Mean SLA	**217.465**	**23.512**	**9.249**	**6.65E-15**	**14.602**	**5.056**	**2.888**	**4.80E-03**	**-36.432**	**9.938**	**-3.666**	**4.06E-04**
Soil	SF	Mean SLA	**185.451**	**21.911**	**8.464**	**2.75E-13**	*9.049*	*5.264*	*1.719*	*0.089*	**-19.448**	**5.650**	**-3.442**	**8.54E-04**
Soil	SJ	Mean SLA	**176.075**	**15.284**	**11.521**	**1.12E-20**	0.873	2.729	0.320	0.750	**-16.524**	**6.897**	**-2.396**	**0.018**

Table 7. (continued)

Model	Species	Response	β_{Int}	SE_{Int}	t_{Int}	p_{Int}	β_{G}	SE_{G}	t_{G}	p_{G}	β_{CII}	SE_{CII}	t_{CII}	p_{CII}
Soil	PT	Mean [Chl]	**32.570**	**5.478**	**5.946**	**3.72E-08**	*1.695*	*1.010*	*1.679*	*0.096*	**-4.735**	**2.309**	**-2.050**	**0.043**
Soil	SA	Mean [Chl]	12.851	14.352	0.895	0.373	7.692	6.660	1.155	0.251	*15.833*	*9.002*	*1.759*	*0.082*
Soil	SF	Mean [Chl]	**45.881**	**6.526**	**7.030**	**1.89E-10**	**-4.519**	**1.599**	**-2.826**	**0.006**	**-4.253**	**1.701**	**-2.500**	**0.014**
Soil	SJ	Mean [Chl]	**36.425**	**3.861**	**9.433**	**7.24E-16**	0.518	0.690	0.751	0.454	-0.047	1.743	-0.027	0.978
Soil	PT	Total [N]	**10.464**	**2.663**	**3.929**	**1.92E-04**	0.299	0.438	0.684	0.496	-0.463	1.004	-0.461	0.646
Soil	SA	Total [N]	**14.450**	**1.315**	**10.987**	**8.85E-19**	0.269	0.283	0.951	0.344	0.117	0.556	0.210	0.834
Soil	SF	Total [N]	**8.506**	**2.090**	**4.069**	**9.57E-05**	-0.130	0.502	-0.259	0.796	0.691	0.540	1.279	0.204
Soil	SJ	Total [N]	**12.008**	**1.189**	**10.099**	**2.12E-17**	0.314	0.212	1.476	0.143	0.458	0.537	0.854	0.395
Soil	PT	Total [P]	**1.076**	**0.192**	**5.610**	**3.42E-07**	-0.005	0.032	-0.147	0.883	-0.063	0.072	-0.868	0.388
Soil	SA	Total [P]	**0.916**	**0.103**	**8.866**	**3.48E-14**	-0.001	0.022	-0.049	0.961	-0.064	0.044	-1.455	0.149
Soil	SF	Total [P]	**1.136**	**0.148**	**7.699**	**1.11E-11**	*-0.061*	*0.035*	*-1.733*	*0.086*	**-0.082**	**0.038**	**-2.161**	**0.033**
Soil	SJ	Total [P]	**0.592**	**0.155**	**3.812**	**2.28E-04**	**0.190**	**0.093**	**2.049**	**0.043**	0.022	0.088	0.247	0.805
Soil	PT	Total [K]	**12.148**	**1.403**	**8.661**	**8.07E-13**	-0.283	0.231	-1.226	0.224	-0.517	0.529	-0.978	0.331
Soil	SA	Total [K]	**10.527**	**1.146**	**9.189**	**6.96E-15**	**0.564**	**0.247**	**2.289**	**0.024**	**-2.443**	**0.485**	**-5.041**	**2.12E-06**
Soil	SF	Total [K]	**16.149**	**1.777**	**9.088**	**1.15E-14**	-0.431	0.427	-1.009	0.315	**-2.281**	**0.459**	**-4.966**	**2.89E-06**
Soil	SJ	Total [K]	**5.538**	**2.058**	**2.691**	**0.008**	2.005	1.232	1.628	0.106	1.275	1.165	1.094	0.276

Table 7. (continued)

Model	Species	Response	$\beta_{G\times C}$	$SE_{G\times C}$	$t_{G\times C}$	$p_{G\times C}$	β_{BA}	SE_{BA}	t_{BA}	p_{BA}	δInc-MSE_{G}	δInc-MSE_{CII}	δInc-MSE_{BA}	RF pseudo-R^2
Soil	PT	Height RGR	-3.63E-03	3.30E-03	-1.099	0.274					-0.059	0.152	0.076	0.076
Soil	SA	Height RGR	**-0.008**	**3.26E-03**	**-2.434**	**0.017**					0.030	0.109	0.065	0.014
Soil	SF	Height RGR	*-0.005*	*3.01E-03*	*-1.722*	*0.088*	*-0.127*	*0.076*	*-1.663*	*0.099*	0.046	0.232	0.143	0.211
Soil	SJ	Height RGR	**-0.012**	**3.27E-03**	**-3.745**	**2.88E-04**					0.051	0.259	0.252	0.245
Soil	PT	D_{base} RGR	3.16E-03	3.12E-03	1.010	0.315					-0.037	0.280	0.106	0.099
Soil	SA	D_{base} RGR	-3.49E-03	2.75E-03	-1.267	0.208	**-0.242**	**0.110**	**-2.207**	**0.030**	-0.042	0.309	0.027	0.155
Soil	SF	D_{base} RGR	**-0.008**	**3.20E-03**	**-2.626**	**0.010**					-0.100	0.159	0.141	0.141
Soil	SJ	D_{base} RGR	**-0.007**	**3.52E-03**	**-1.997**	**0.048**					-0.019	0.277	0.169	0.149
Soil	PT	$\log_{10}$(TLA)	0.005	0.007	0.733	0.465					0.087	0.349	0.112	0.209
Soil	SA	$\log_{10}$(TLA)	-0.006	0.006	-1.044	0.299	*-0.464*	*0.235*	*-1.974*	*0.051*	0.088	0.218	0.107	0.088
Soil	SF	$\log_{10}$(TLA)	**-0.021**	**0.007**	**-2.748**	**0.007**	**-0.429**	**0.190**	**-2.256**	**0.026**	0.016	0.275	0.210	0.265
Soil	SJ	$\log_{10}$(TLA)	**-0.026**	**0.008**	**-3.477**	**7.25E-04**					-0.005	0.337	0.217	0.217
Soil	PT	Mean SLA	4.03E-03	0.757	0.005	0.996					0.087	0.144	0.096	0.011
Soil	SA	Mean SLA	**1.233**	**0.537**	**2.295**	**0.024**					0.217	0.204	0.155	0.210
Soil	SF	Mean SLA	-0.068	0.474	-0.143	0.886					0.015	0.118	-0.038	0.045
Soil	SJ	Mean SLA	**1.404**	**0.399**	**3.520**	**6.26E-04**					0.033	0.185	0.251	0.127

Table 7. (continued)

Model	Species	Response	$\beta_{G\times C}$	$SE_{G\times C}$	$t_{G\times C}$	$p_{G\times C}$	β_{BA}	SE_{BA}	t_{BA}	p_{BA}	δInc-MSE_G	δInc-MSE_{CII}	δInc-MSE_{BA}	RF pseudo-R^2
Soil	PT	Mean [Chl]	0.134	0.169	0.790	0.431					-0.043	0.012	0.123	0.017
Soil	SA	Mean [Chl]	-0.121	0.109	-1.105	0.272	*-7.498*	*4.371*	*-1.715*	*0.089*	0.244	-0.056	-0.016	0.017
Soil	SF	Mean [Chl]	0.065	0.141	0.462	0.645					0.213	0.134	-0.089	0.025
Soil	SJ	Mean [Chl]	**-0.347**	**0.101**	**-3.443**	**8.13E-04**					-0.079	-0.051	0.225	-0.007
Soil	PT	Total [N]	0.084	0.081	1.036	0.303					0.037	0.126	0.123	0.039
Soil	SA	Total [N]	**-0.103**	**0.030**	**-3.442**	**8.49E-04**					-0.062	1.45E-03	0.239	0.029
Soil	SF	Total [N]	**0.101**	**0.045**	**2.230**	**0.028**					-0.002	0.108	0.071	-0.002
Soil	SJ	Total [N]	-0.038	0.031	-1.230	0.221					0.064	0.012	0.138	0.007
Soil	PT	Total [P]	-3.96E-03	0.006	-0.680	0.499					-0.045	0.064	0.200	0.046
Soil	SA	Total [P]	-2.06E-04	2.35E-03	-0.088	0.930					-0.015	0.048	0.091	-0.051
Soil	SF	Total [P]	-2.26E-03	3.20E-03	-0.707	0.482					0.075	0.103	0.268	0.155
Soil	SJ	Total [P]	**0.007**	**2.26E-03**	**3.124**	**2.28E-03**	*-0.107*	*0.061*	*-1.745*	*0.084*	0.137	-3.09E-03	0.253	0.132
Soil	PT	Total [K]	**-0.089**	**0.043**	**-2.098**	**0.039**					-0.045	0.063	0.137	-0.063
Soil	SA	Total [K]	**0.080**	**0.026**	**3.054**	**2.90E-03**					0.184	0.328	0.159	0.263
Soil	SF	Total [K]	-0.048	0.039	-1.241	0.217					-0.093	0.206	0.138	0.126
Soil	SJ	Total [K]	**0.085**	**0.030**	**2.848**	**0.005**	-1.217	0.809	-1.504	0.135	-0.022	-0.066	0.103	-0.020

Alpha diversity response model results

Table 8. Leaf symptom morphological species response modeling results, with AIC_c, mean and SE of 5-fold cross-validation RMSE, and Random Forest statistics. Significant (p<0.05) effects in bold, close-to-significant (p<0.10) effects in italic. Estimated, reference, and residual *df* as df_{Est}, df_{Ref}, and df_{Res}, respectively. Partial-R^2 as p-R^2.

Model	Species	Response	n	AIC_c	$RMSE_{CV}$	SE_{RMSE}	R^2_{adj}	Dev_{Expl}	df_{Est}	df_{Ref}	F_{Smooth}	p_{Smooth}	df_{Res}
Elevation	PT	D_0	105	463.508	2.223	0.028	0.109	0.135	1.000	1.001	0.566	0.454	101.000
Elevation	SA	D_0	102	513.785	1.790	0.025	0.047	0.085	1.000	1.000	0.691	0.408	97.000
Elevation	SF	D_0	113	541.136	1.503	0.020	0.165	0.188	1.000	1.000	1.753	0.188	109.000
Elevation	SJ	D_0	115	557.502	2.947	0.048	0.150	0.187	1.916	1.993	**6.854**	**0.002**	109.084
Elevation	PT	D_1	105	418.762	2.066	0.025	0.100	0.126	1.000	1.000	0.449	0.504	101.000
Elevation	SA	D_1	102	439.898	1.785	0.019	-0.025	0.006	1.000	1.001	0.189	0.665	98.000
Elevation	SF	D_1	113	478.387	2.638	0.031	0.074	0.099	1.000	1.000	1.049	0.308	109.000
Elevation	SJ	D_1	115	505.721	1.977	0.023	0.126	0.164	1.918	1.993	**7.047**	**0.002**	109.082
Elevation	PT	D_2	105	382.509	1.641	0.018	0.094	0.120	1.000	1.000	0.377	0.541	101.000
Elevation	SA	D_2	102	408.716	2.777	0.033	-0.021	0.011	1.164	1.302	0.039	0.878	97.836
Elevation	SF	D_2	113	435.595	2.193	0.029	0.030	0.056	1.000	1.000	0.399	0.529	109.000
Elevation	SJ	D_2	115	478.730	1.946	0.020	0.111	0.149	1.906	1.991	**6.008**	**0.004**	109.094

Table 8. (continued)

Model	Species	Response	p-R^2_{Int}	p-R^2_{Smooth}	p-R^2_{G}	p-R^2_{CII}	p-R^2_{BA}	p-$R^2_{\text{C×B}}$	β_{Int}	SE_{Int}	t_{Int}	p_{Int}	β_{G}	SE_{G}	t_{G}	p_{G}
Elevation	PT	D_0	5.73E-04	0.006		0.137	0.137		0.279	1.160	0.240	0.811				
Elevation	SA	D_0	0.101	0.007		0.023	0.040	0.000	**13.698**	**4.151**	**3.300**	**1.35E-03**				
Elevation	SF	D_0	0.060	0.016		0.102	0.102		**4.384**	**1.663**	**2.635**	**0.010**				
Elevation	SJ	D_0	0.061	0.115		3.44E-03	0.032	0.000	**11.416**	**4.282**	**2.666**	**0.009**				
Elevation	PT	D_1	1.07E-03	0.004		0.111	0.111		0.309	0.938	0.329	0.743				
Elevation	SA	D_1	0.140	1.93E-03		7.73E-05	7.73E-05		**5.209**	**1.305**	**3.990**	**1.27E-04**				
Elevation	SF	D_1	0.079	0.010		0.059	0.059		**3.843**	**1.260**	**3.049**	**2.88E-03**				
Elevation	SJ	D_1	0.077	0.118		0.018	0.036	0.000	**10.340**	**3.419**	**3.025**	**3.10E-03**				
Elevation	PT	D_2	0.003	3.72E-03		0.090	0.090		0.407	0.789	0.516	0.607				
Elevation	SA	D_2	0.165	4.32E-03		0.006	0.006		**4.983**	**1.118**	**4.459**	**2.20E-05**				
Elevation	SF	D_2	0.089	3.65E-03		0.040	0.040		**3.398**	**1.043**	**3.258**	**1.49E-03**				
Elevation	SJ	D_2	0.073	0.103		0.022	0.031	0.000	**8.949**	**3.040**	**2.944**	**3.96E-03**				

Table 8. (continued)

Model	Species	Response	β_{CII}	$\mathrm{SE}_{\mathrm{CII}}$	t_{CII}	p_{CII}	β_{BA}	$\mathrm{SE}_{\mathrm{BA}}$	t_{BA}	p_{BA}	$\beta_{\mathrm{C\times B}}$	$\mathrm{SE}_{\mathrm{C\times B}}$	$t_{\mathrm{C\times B}}$	$p_{\mathrm{C\times B}}$	δInc-$\mathrm{MSE}_{\mathrm{G}}$	δInc-$\mathrm{MSE}_{\mathrm{CII}}$	δInc-$\mathrm{MSE}_{\mathrm{BA}}$	RF pseudo-R^2
Elevation	PT	D_0	**1.987**	**0.515**	**3.854**	**2.04E-04**	0.035	0.038	0.922	0.359					0.042	0.252	0.060	0.091
Elevation	SA	D_0	-3.944	2.606	-1.514	0.133	**-0.469**	**0.233**	**-2.015**	**0.047**	**0.330**	**0.148**	**2.237**	**0.028**	-0.034	0.065	0.134	-0.019
Elevation	SF	D_0	**2.079**	**0.594**	**3.500**	**6.76E-04**	-0.067	0.050	-1.350	0.180					-0.158	0.178	0.024	-0.013
Elevation	SJ	D_0	-1.603	2.577	-0.622	0.535	*-0.420*	*0.221*	*-1.897*	*0.061*	*0.228*	*0.136*	*1.672*	*0.097*	0.112	0.177	-0.027	0.035
Elevation	PT	D_1	**1.450**	**0.417**	**3.481**	**7.40E-04**	0.051	0.031	1.625	0.107					-0.033	0.200	0.080	0.012
Elevation	SA	D_1	0.060	0.691	0.087	0.931	0.022	0.037	0.587	0.558					0.086	-0.054	0.054	-0.040
Elevation	SF	D_1	**1.160**	**0.450**	**2.579**	**0.011**	-0.021	0.038	-0.556	0.580					-0.187	0.099	-0.049	-0.131
Elevation	SJ	D_1	-2.884	2.057	-1.402	0.164	**-0.357**	**0.177**	**-2.021**	**0.046**	**0.239**	**0.109**	**2.202**	**0.030**	0.177	0.156	-0.045	0.023
Elevation	PT	D_2	**1.081**	**0.350**	**3.085**	**2.62E-03**	**0.056**	**0.026**	**2.143**	**0.034**					-0.068	0.159	0.091	-1.33E-03
Elevation	SA	D_2	-0.450	0.592	-0.760	0.449	0.013	0.032	0.408	0.684					0.089	-0.056	-0.022	-0.074
Elevation	SF	D_2	**0.779**	**0.372**	**2.093**	**0.039**	-0.003	0.031	-0.090	0.928					-0.201	0.035	-0.104	-0.191
Elevation	SJ	D_2	-2.852	1.829	-1.559	0.122	*-0.291*	*0.157*	*-1.852*	*0.067*	**0.212**	**0.097**	**2.190**	**0.031**	0.145	0.146	4.90E-03	0.028

Table 8. (continued)

Model	Species	Response	n	AIC$_c$	RMSE$_{CV}$	SE$_{RMSE}$	R^2_{adj}	Dev$_{Expl}$	df_{Est}	df_{Ref}	F_{Smooth}	p_{Smooth}	df_{Res}
Soil	PT	D_0	105	462.196	2.198	0.028	0.120	0.146	1.000	1.000	1.843	0.178	101.000
Soil	SA	D_0	102	515.916	1.770	0.024	0.015	0.045	1.000	1.001	1.368	0.245	98.000
Soil	SF	D_0	113	541.925	1.488	0.020	0.160	0.182					109.000
Soil	SJ	D_0	115	563.107	2.964	0.050	0.108	0.145	1.702	1.911	**3.037**	**0.034**	109.298
Soil	PT	D_1	105	417.340	2.066	0.027	0.112	0.138	1.000	1.000	1.832	0.179	101.000
Soil	SA	D_1	102	439.755	1.775	0.019	-0.023	0.007	1.001	1.002	0.327	0.569	97.999
Soil	SF	D_1	113	478.973	2.639	0.032	0.069	0.094					109.000
Soil	SJ	D_1	115	511.599	1.982	0.024	0.080	0.117	1.591	1.832	**3.071**	**0.033**	109.409
Soil	PT	D_2	105	380.840	1.639	0.018	0.108	0.134	1.000	1.000	2.000	0.160	101.000
Soil	SA	D_2	102	408.599	2.837	0.033	-0.022	0.009	1.083	1.160	0.029	0.898	97.917
Soil	SF	D_2	113	435.862	2.248	0.029	0.028	0.054					109.000
Soil	SJ	D_2	115	483.911	1.996	0.021	0.069	0.106	1.499	1.749	*2.541*	*0.055*	109.501

Table 8. (continued)

Model	Species	Response	p-R^2_{Int}	p-R^2_{Smooth}	p-R^2_{G}	p-R^2_{CII}	p-R^2_{BA}	p-$R^2_{C\times B}$	β_{Int}	SE_{Int}	t_{Int}	p_{Int}	β_{G}	SE_{G}	t_{G}	p_{G}
Soil	PT	D_0	6.03E-04	0.018		0.148	0.148		0.285	1.153	0.247	0.806				
Soil	SA	D_0	0.082	0.014		0.018	0.018		**5.671**	**1.922**	**2.951**	**3.96E-03**				
Soil	SF	D_0	0.049		0.009	0.107	0.107		**5.396**	**2.277**	**2.370**	**0.020**	-0.553	0.558	-0.991	0.324
Soil	SJ	D_0	0.068	0.069		0.006	0.035	0.000	**12.265**	**4.377**	**2.802**	**6.00E-03**				
Soil	PT	D_1	1.13E-03	0.018		0.119	0.119		0.314	0.931	0.337	0.737				
Soil	SA	D_1	0.140	0.003		2.32E-05	2.32E-05		**5.293**	**1.323**	**4.001**	**1.23E-04**				
Soil	SF	D_1	0.055		0.004	0.062	0.062		**4.344**	**1.723**	**2.521**	**0.013**	-0.292	0.422	-0.692	0.491
Soil	SJ	D_1	0.086	0.068		0.024	0.040	0.000	**11.125**	**3.499**	**3.179**	**1.92E-03**				
Soil	PT	D_2	2.74E-03	0.019		0.089	0.089		0.412	0.783	0.527	0.600				
Soil	SA	D_2	0.167	0.002		0.006	0.006		**5.016**	**1.134**	**4.423**	**2.52E-05**				
Soil	SF	D_2	0.055		0.001	0.042	0.042		**3.600**	**1.424**	**2.528**	**0.013**	-0.130	0.349	-0.374	0.709
Soil	SJ	D_2	0.082	0.057		0.028	0.034	0.000	**9.612**	**3.104**	**3.097**	**2.48E-03**				

Table 8. (continued)

Model	Species	Response	β_{CII}	SE_{CII}	t_{CII}	p_{CII}	β_{BA}	SE_{BA}	t_{BA}	p_{BA}	$\beta_{C\times B}$	$SE_{C\times B}$	$t_{C\times B}$	$p_{C\times B}$	δInc-MSE_G	δInc-MSE_{CII}	δInc-MSE_{BA}	RF pseudo-R^2
Soil	PT	D_0	**1.957**	**0.512**	**3.822**	**2.29E-04**	0.037	0.038	0.978	0.330					0.021	0.252	0.070	0.071
Soil	SA	D_0	1.356	1.007	1.347	0.181	0.032	0.054	0.583	0.561					0.017	0.083	0.162	1.91E-03
Soil	SF	D_0	**2.134**	**0.593**	**3.596**	**4.86E-04**	-0.059	0.049	-1.207	0.230					0.020	0.224	0.118	0.095
Soil	SJ	D_0	-2.151	2.629	-0.818	0.415	*-0.441*	*0.226*	*-1.946*	*0.054*	*0.241*	*0.139*	*1.732*	*0.086*	0.019	0.157	-0.071	-0.017
Soil	PT	D_1	**1.427**	**0.414**	**3.451**	**8.17E-04**	*0.052*	*0.031*	*1.684*	*0.095*					-0.030	0.205	0.077	0.032
Soil	SA	D_1	0.034	0.693	0.049	0.961	0.020	0.037	0.530	0.598					-0.077	-0.058	-0.010	-0.112
Soil	SF	D_1	**1.199**	**0.449**	**2.669**	**0.009**	-0.016	0.037	-0.427	0.670					-0.062	0.172	0.018	1.63E-03
Soil	SJ	D_1	-3.376	2.102	-1.606	0.111	**-0.375**	**0.181**	**-2.074**	**0.040**	**0.250**	**0.111**	**2.251**	**0.026**	0.063	0.118	-0.068	-0.022
Soil	PT	D_2	**1.063**	**0.348**	**3.057**	**0.003**	**0.057**	**0.026**	**2.206**	**0.030**					-0.057	0.174	0.078	0.008
Soil	SA	D_2	-0.451	0.594	-0.759	0.450	0.011	0.032	0.359	0.720					-0.089	-0.077	-0.135	-0.137
Soil	SF	D_2	**0.803**	**0.371**	**2.163**	**0.033**	4.78E-05	0.031	1.56E-03	0.999					-0.112	0.097	-0.050	-0.071
Soil	SJ	D_2	*-3.264*	*1.864*	*-1.751*	*0.083*	*-0.306*	*0.161*	*-1.906*	*0.059*	**0.220**	**0.099**	**2.234**	**0.027**	0.094	0.142	-2.84E-05	2.38E-03

Appendix 8

Leaf symptom morphological species inventory summary

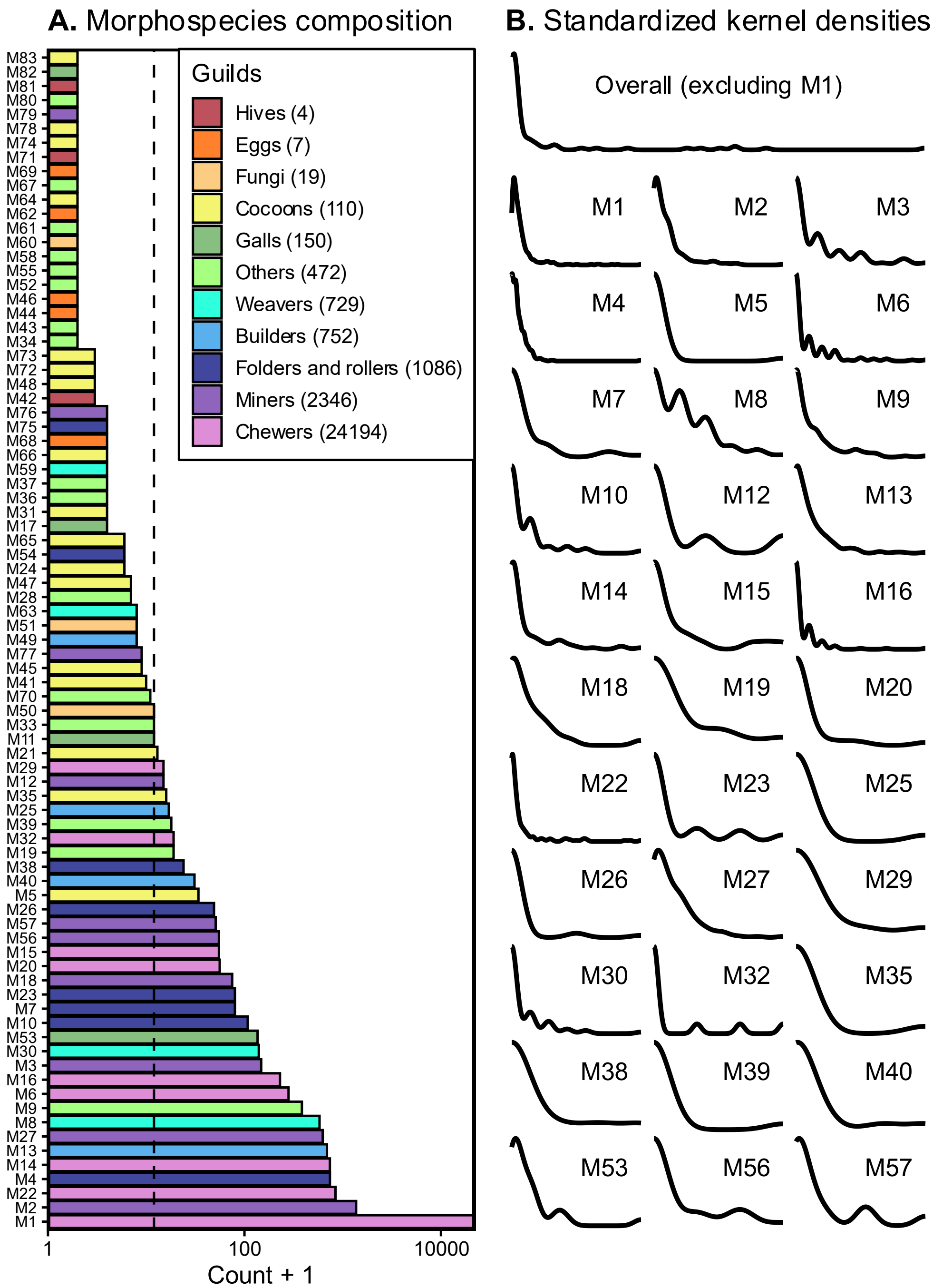


Figure 35. **A.** Leaf morphospecies counts (29869 in total, 7946 without M1) and guild compositions with total abundance in parentheses (note that the horizontal

axis is $\log_{10}$-scaled). **B.** Standardized leaf morphospecies kernel densities (with equal gaussian kernels and bandwidths); excluding M1 from the overall plot to avoid skewness. Only showing species-wise densities for morphospecies with >12 total counts (dashed line=12 in **A.**) and sufficient count variance for density smoothing (e.g. M21 only had counts of 1). M1 was excluded from all analyses.

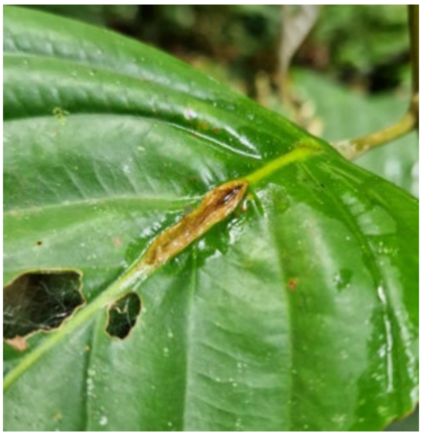
Leaf symptom morphological species list

Table 9. Leaf symptom morphological species. IDs, names, general descriptions, total counts, and guilds, with corresponding type examples.

ID	Name	Description	Count	Group	Type example
M1	General folivory	Folivory without discernible patterns.	21957	Chewers	
M2	Blotch miners	Reddish-brown miner blotches without discernable patterns.	1370	Miners	
M3	Growing tracks	Miner tracks growing in width from about <1 to 3 mm over distance.	147	Miners	
M4	Edge fold	Edge of the leaf folded, either dorsally or ventrally.	740	Folders and rollers	

M5	Hanging cocoon	Cocoons hanging on stipules from the leaf, ventrally.	33	Cocoons	
M6	Main vein cut	Main vein of the leaf cut off, with terminal half remaining.	282	Chewers	
M7	Main vein fold	Fold along the main vein, either dorsally or ventrally.	79	Folders and rollers	
M8	White silk	General cover of white silk anywhere on the leaf that does not produce any other morphospecies, includes spider webs.	580	Weavers	

M9	Hanging tails	Dark, somewhat loose, tail-looking structure, hanging from the ventral side of the leaf. Can be short or very long. Similar texture to old rubber bands, but softer.	397	Others	
M10	Rolled cylinder	Leaf cut out along the main vein and rolled into a hanging cylinder.	108	Folders and rollers	
M11	Small dark ball (ventral)	Small dark button-like balls on the ventral side of the leaf. Likely galls.	11	Galls	
M12	Larger tracks	Miner tracks constantly about 3 to 5 mm wide. Direction seemingly random, but often contained by side veins.	15	Miners	

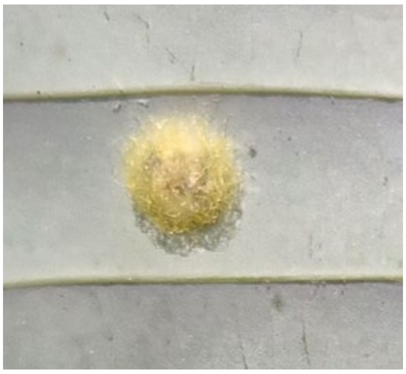
M13	Terminal arrow	Tip of the leaf cut out, and often folded along the main vein, arrow-like.	699	Builders	
M14	Big edge bites	Big half-circle cutouts, about 2 to 3 cm wide, along the edges of the leaf.	739	Chewers	
M15	Excavation	Main or side vein cut open but not eaten, leaving a noticeable scar.	56	Chewers	
M16	Tip eaten	Tip of the leaf eaten, either clean or rough, across the main vein.	229	Chewers	

M17	Spikey gall	Spikey ball, likely a gall, stuck to the stem or a stipule, with firm/hard shell.	3	Galls	
M18	Thin tracks	Miner tracks constantly about 1 to 2 mm wide, often perpendicular to each other.	74	Miners	
M19	Shotgun pellets	Circular holes through the leaf, about 1 to 3 mm in diameter, without consistent clustering.	18	Others	

M20	Main vein eaten	Main vein eaten, like counterfeit split.	55	Chewers	
M21	Tubed chamber	Tubed, semi-hard shelled, chamber growing on the surface of the ventral side of the leaf, often between veins. Cocoon? Chrysalis?	13	Cocoons	
M22	Hourglass herbivory	Convex folivory from both sides of the leaf, leaving its shape distinctly hourglass-looking.	843	Chewers	
M23	Cross-rolled cylinder	Leaf cut across or along side vein and rolled into a non-hanging cylinder.	79	Folders and rollers	

M24	Ventral resupinate cocoon on vein	Cocoon hanging on the surface of the ventral side of the leaf, either along main or side veins.	5	Cocoons	
M25	Fused leaves	Multiple leaves (can be more than two) woven together by silk.	16	Builders	
M26	Terminal fold	Tip of the leaf folded, either dorsally or ventrally.	48	Folders and rollers	
M27	Crust eaters	Miner tracks leading from the interior to the edge of the leaf, where the sides have been eaten.	625	Miners	

M28	Ventral spikey club	Spikey club-looking structure on the ventral side of the leaf, sometimes fastened with silk. Termite?	6	Others	
M29	Cornucopia	Terminal half of the leaf cut out or eaten cleanly across. The main vein is left, curled ventrally, and black in color to the across-cut. The remaining base half of the leaf is slightly folded dorsally, making the leaf cornucopia-like.	14	Chewers	
M30	Threads	White thread-like structures. Often residues remaing around the main structures. Sometimes on stipules. Ants?	139	Weavers	
M31	Big cocoon	Big, about 4×3 cm, elliptical tan-colored cocoon along the surface of the ventral side of the leaf.	3	Cocoons	

M32	Main vein de-barker	Epidermal phagy on the main vein, both dorsal and ventral.	19	Chewers	
M33	Hardened slime trails	Transparent hardened trails on the dorsal side of the leaf.	11	Others	
M34	Long chamber	Very long and compact chamber stretching along the main vein on the ventral side of the leaf. Large chrysalis?	1	Others	
M35	Small furry balls (ventral), green	Very small, around 2 to 4 mm in diameter, green furry balls.	15	Cocoons	

M36	Dorsal mound	Termite-like mound on the dorsal side of the leaf.	3	Others	
M37	Acorn cocoon	Acorn-like chamber with hard shell.	3	Others	
M38	Rolled leaf	The whole leaf is rolled along the main vein; not folded.	23	Folders and rollers	
M39	Ventral mound	Leaf-like mound on the ventral side of the leaf. Similar to M36 but ventral. Termite?	16	Others	
M40	Folded leaf cut-outs	Pieces of leaves folded on each other with silk.	30	Builders	

M41	Small white ventral cocoon	Very small, white, and silky cocoon on the ventral side of the leaf.	9	Cocoons	
M42	Clay hive	Clay-like ball, with sporadically placed holes (entrances?) about 2 to 3 mm in diameter, hanging from the ventral side of the leaf. Termite?	2	Hives	
M43	Barnacle chambers	Barnacle-like cluster of small chambers.	1	Others	
M44	Green capsules	Small and soft green balls (eggs?) suspended by thin white antannea on the ventral side of the leaf.	1	Eggs	

M45	Big white hairy cocoon	Big, about 2×4 cm, white cocoon covered in white, gray, and black hairs.	8	Cocoons	
M46	Rice grains	Rice grain-looking buttons attached to the ventral side of the leaf. Likely eggs.	1	Eggs	
M47	Black chamber	Small black chambers, either dorsally or ventrally attached.	6	Cocoons	
M48	Dirt chamber	Looks like a dirt-covered cocoon. Not too small, maybe about 2 to 3 mm long.	2	Cocoons	

M49	Rolled leaf chamber	Chamber made up of rolled leaf residues. Attached ventrally.	7	Builders	
M50	*Cordyceps* victim	Any invertebrate victim of a pathogenic *Cordyceps* Fr. sp. fungus stuck to the leaf. Flies, wasps, ants, and moths were observed victims.	11	Fungi	
M51	Small white fruiting bodies	Fungus infection: small white fruiting bodies and thin hyphae along stem and petioles.	7	Fungi	

M52	Small "stars"	Small and flat circular buttons (eggs?) with tails; star-like.	1	Others	
M53	Edge crust	Edge of the leaf covered in small gall-like complexes, about 0.5 to 1 mm in diameter each, causing the edge of the leaf to crumple and start folding.	135	Galls	
M54	Leaf fortress	Leaf cut out close to the main vein, folded either dorsally or ventrally, and fused on itself. The folded part of the leaf is often brown in color.	5	Folders and rollers	
M55	Black glass	Fragile, but not loose, crust. Deep purple, brown, and blackish in color, leaving a trailed along the veins on the dorsal side of the leaf. Excrement? Shedding residues?	1	Others	

M56	Giant tracks	Giant miner tracks growing in size from about 2 mm to 1.5 cm wide, while zig-zagging along the edge of the leaf, very commonly across the main vein at the leaf tip.	53	Miners	
M57	Side vein eaters	Miner tracks on the side veins on the dorsal side of the leaf.	50	Miners	
M58	Raisin	Black compact, hard, raisin-looking ball with ridges. Attached to the dorsal side of the leaf by thick silk.	1	Others	
M59	Milk cocoon	A "pool" of white silk on the dorsal side of the leaf.	3	Weavers	

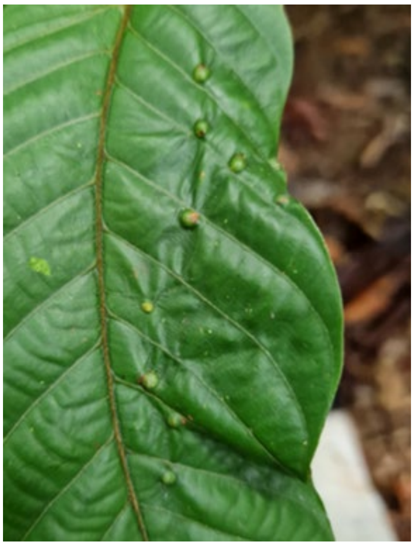
M60	Rusty dust	Rust-colored dust on the dorsal side of the leaf.	1	Fungi	
M61	Short chamber	Compact short and hard shell, stuck to the main vein on the ventral side of the leaf; greenish-white scales with black dots.	1	Others	
M62	Green smooth small button (ventral)	Small compact, translucent, green button on the ventral side of the leaf. Likely eggs.	1	Eggs	
M63	Big spun nest	Huge woven nest, often incorporating multiple leaves or entire small branches. Weaver ants?	7	Weavers	
M64	Big soft green netted cocoon	Big green cocoon made out of silky netting. Not compact; easy to squeeze.	1	Cocoons	

M65	Small furry balls (ventral), white	Very small, around 2 to 4 mm in diameter, white furry balls. Cocoons? Eggs?	5	Cocoons	
M66	Clay chamber	Clay-like, in color and texture, chamber on the ventral side of the leaf; oblong body close to the main vein.	3	Cocoons	
M67	Standing chamber	Larva-like chamber standing on the dorsal side of the leaf. Green and grayish-brown stripes along the stretched body.	1	Others	
M68	Beach balls	Transparent beach ball-looking shells on the ventral side of the leaf, about 2 to 4 mm wide. Likely eggs.	3	Eggs	

M69	Thin rice grain buttons	Gray rice grain-like buttons stuck to the ventral side of the leaf, about 2 to 4 mm wide. Likely eggs.	1	Eggs	
M70	Tooth marks	Straight tooth-mark-looking indents across the dorsal side of the leaf. Similar to a bite, but not quite gnawed through.	10	Others	
M71	Wasp nest	Wasp nest-like ball, fragile in texture and structure, stuck to the ventral side of the leaf.	1	Hives	
M72	Webbed cocoon (dorsal)	Webbed cocoon, tan-colored, on the dorsal side of the leaf.	2	Cocoons	

M73	Fat brown chamber (ventral)	Compact brown chamber on the ventral side of the leaf. Not hanging but not quite resupinate; somewhere in-between. Somewhat shiny, almost fatty. Chrysalis?	2	Cocoons	
M74	Small yellow cocoon (ventral)	Small cocoon, pale-yellow, stuck to the ventral side of the leaf, around 2×4 mm.	1	Cocoons	
M75	Mid-leaf fold	Silk folding the middle of the leaf along the side veins.	4	Folders and rollers	
M76	Tiny edge tracks	Small, around 1 to 2 mm in diameter, tracks in complex patterns along the edge of the leaf.	3	Miners	

M77	Terminal skeletonizer	Miner blotch at the tip of the leaf, distinctively leaving the vein tissue, with associated thin, <1 mm wide, tracks in complex patterns in its periphery.	8	Miners	
M78	Silk-covered compact ventral chamber	Brown chamber on the ventral side of the leaf, covered in white silk.	1	Cocoons	
M79	Main vein crawlers	Thin, about 1 to 2 mm wide, miner tracks along the main vein, branching out along the side veins sporadically.	1	Miners	
M80	Scissor cut	Leaf cut clean, splitting the main vein.	1	Others	

M81	White egg hive	Small hive, about 5 to 6 mm wide, of really small, <1 mm in diameter, translucent white buttons. Clusters of eggs?	1	Hives	
M82	Leaf galls	Small galls, about 1 to 2 mm in diameter, covering the leaf sporadically.	1	Galls	
M83	Skeletal chamber	Chamber with skeletal structure, almost rib cage-like, green-yellowish color, on the ventral side of the leaf. Chrysalis?	1	Cocoons	

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