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Edaphic and climatic factors affecting the distribution of *Castanopsis tungurrut* (Blume) A. DC. (Fagaceae) in cibodas biosphere reserve, Indonesia

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Castanopsis tungurrut (Blume) A. DC. (Fagaceae) is an Indonesian native plant species with limited spatial distribution; it is found only in Java, Kalimantan, and Sumatera in lower montane to submontane forests. This species has been classified as endangered by the IUCN, necessitating collection of more information on its habitat and environmental preferences before embarking on conservation planning. Studies on the species' natural habitat are scarce. This study aims to identify the environmental factors (edaphic + climatic factors) influencing the distribution of *C. tungurrut* along an altitudinal gradient in the Cibodas Biosphere Reserve. The nested plot method was applied to assess the forest vegetation at an altitudinal range of ca. 750–1800 m asl. Environmental factors were measured using portable equipment and through laboratory analysis. Ordination technique using canonical correspondence analysis (CCA) was utilised to pinpoint the environmental factors influencing the species' distribution based on basal area. CCA showed temperature to be the most limiting factor affecting the distribution. Edaphic factors – cation exchange capacity, content of carbon, nitrogen, phosphorus, and potassium, and soil pH – had less influence. Thus, it can be inferred that dependence of *C. tungurrut* on temperature determines its distribution pattern in its natural habitat, like *Ostodes paniculata* and *Sloanea sigun*. In contrast, the distribution of *Castanopsis javanica, Castanopsis argentea, Schima wallichii, Altingia excelsa, Dacrycarpus imbricatus, Cestrum aurantiacum*, and *Castanopsis acuminatissima* was found to be more influenced by edaphic factors than by climatic factors.

Keywords: *Castanopsis tungurrut,* species composition, altitudinal gradient, environmental factors

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INTRODUCTION

The distribution of plant species is intricately linked to a multitude of factors, including predation, competition, human activity, and climate, which shape their survival, growth, and reproductive success. Specifically, temperature, altitude, and water availability are climatic factors that limit species distribution (Box, 1995; Buot and Osumi, 2011; Martinez and Buot, 2018; Villanueva and Buot, 2018; Caringal et al., 2021). Understanding these factors and their impact on specific plant species is crucial for predicting and managing the ecological dynamics of diverse ecosystems.

Castanopsis tungurrut, commonly known as 'tungurut', 'kalimorot', 'tunggeureuk', or 'tunggurut' in Indonesia, is an endangered plant species known for its ecological significance and unique adaptations to specific environmental conditions. Its distribution is directly affected by environmental conditions such as temperature, humidity, organic carbon (C-organic) level, total nitrogen (N total), cation exchange capacity (CEC), and pH (Zuhri and Mutaqien, 2011; Nurcahyani, 2017). This study examines the environmental factors (edaphic + climatic factors) influencing its distribution in the following four different locations of the Cibodas Biosphere Reserve: Cibodas, Cisarua, Selabintana, and Bodogol. This can help gain insights into broader ecological processes, potentially improving conservation efforts for *C. tungurrut* and other related plant species in the park.

Harapan et al. (2022) claimed that the most important variables for predicting the distribution of *C. tungurrut* are elevation, temperature seasonality, and precipitation in the warmest quarter. This species' distribution has been limited to an altitudinal range of 1400–1800 m asl in Sumatera and 1000–1800 m asl in Java, and it is mostly absent at lower elevations due to human activities, including agriculture and settlement (Simbolon, 2001; Harapan et al., 2022).

Elevation has been regarded as the main limiting factor for the distribution of *C. tungurrut*. A previous study on environmental variables influencing species distribution in the Philippines revealed that species diversity decreases at higher altitudes and that vegetation at lower elevations is much larger and taller than at higher elevations (Buot and Okitsu, 1998). The decrease in species diversity is correlated with insufficient heat at higher altitudes, contributing to the organic production that supports tall trees, a common pattern in tropical forests. Notably, the restricted distribution range of *C. tungurrut* might be correlated with nutrient availability.

Ecologically, *C. tungurrut* has a high frequency with an importance value index (IVI) of 10.14, indicating that the species can adapt to and has a wider tolerance to environmental conditions than other species (Arrijani, 2008). Nevertheless, low regeneration rates can threaten the existence of this species in its natural habitat, as the survival rate was found to be only 33.33% (Handayani et al., 2019).

The low regeneration rate of the species is closely related to its low adaptation to soil nutrients. Several studies have highlighted the importance of root morphology, anatomy, and architecture in adapting to low soil oxygen levels, stress on increase plant resilience, and the role of soil pH in nutrient imbalances and constraints to plant growth on acid soils (Adams, 1981; Puijalon et al., 2008; Pedersen et al., 2020). Therefore, ability to adapt to the environment is a significant factor in a species' existence.

It can be inferred that climatic and edaphic factors are inter-complementary variables influencing the distribution of *C. tungurrut.* Several studies have revealed the complexity of environmental factors affecting the distribution of *Castanopsis* species. Cheuck and Fischer (2021) found that climate change is likely to cause range reductions for some *Castanopsis* species, particularly in marginal tropical zones, due to fragmented forest cover and a lack of efficient seed dispersal mechanisms. Wang et al. (2014) and Yamada and Miyaura (2005) posited that the topography and nut size of *Castanopsis* species contribute to the dominance and spatial genetic structure of the species. Additionally, Wibowo (2006) suggested that *Castanopsis argentea* prefers a habitat with stony soils containing low phosphorus (P) concentrations.

This study aims to identify the environmental factors affecting the distribution pattern of *C. tungurrut* across various altitudinal gradients and to elucidate how specific soil characteristics and climatic variables contribute to the spatial distribution and abundance of the species within the reserve. By understanding these factors, valuable insights into the ecological requirements and habitat preferences of the species will be gained, facilitating informed conservation and management strategies for its preservation.

MATERIALS AND METHODS

Study area

The study site is in Gede Pangrango National Park, Cibodas Biosphere Reserve, West Java, Indonesia. The area encompasses three different regencies: Bogor, Cianjur, and Sukabumi. Cibodas Biosphere Reserve has a total area of 167,000 hectares and is the highest mountain complex on Java Island. The study site is distributed into four different locations: Cibodas, Bodogol, Selabintana, and Cisarua. In this study, the precipitation rate at a location refers to the monthly precipitation average during 2010–2021 (Figure 3). The data showed the lowest precipitation rate in August and the highest in February. The precipitation rate is closely related to the vegetative and generative cycles of a tree's growth. The elevation gradient at each location varied, ranging from 750 to 1800 m asl (Bodogol: 750–1100 m asl, Cibodas: 1300–1800 m asl, Selabintana: 1000–1800 m asl, and Cisarua: 900–1500 m asl), representing the lower and upper montane forest of Gede Pangrango National Park. The locations are bordered by agricultural land and human settlements at lower elevations (ca. less than 1000 m asl) and protected forests at higher elevations. The main vegetation in this forest is Fago-Lauraceous, referred to by Junghuhn and Miquel as a forest at 1000–2400 m asl in Gede Pangrango National Park, with common species being *Acer laurinum, Engelhardia spicata, Schima wallichii, Weinmannia blumei*, and the fern *Cyathea* (Simbolon et al., 2012).

Forest structure analysis

The nested plot method was used for forest structure analysis. Plots of 20 × 20 m were used for trees, 10 x 10 m for poles, 5 x 5 m for saplings, and 2 x 2 m for wildings inside each. The plots were utilised with an elevation gradient of around 750–1800 m asl, and the coordinates were recorded using a GPS device (Garmin eTrex 10). The total number of plots was 41, representing four locations: Bodogol, Cibodas, Cisarua, and Selabintana. Each location had a different number of plots depending on the topography, elevation, and location: 10 for Bodogol, 14 for Cibodas, eight for Cisarua, and nine for Selabintana.

Trees were defined as woody plants with stem diameters greater than 5 cm and heights greater than 2 metres; poles were those whose stands had diameters between 2.5 cm and 5 cm; saplings were the individuals with a height of more than 130 cm and a diameter at breast height (dbh) of less than 2.5 cm; wildings were the individuals with heights less than 130 cm (Newton, 1988; Vargas-Rodriguez et al., 2005; Fathia et al., 2019). All the data recorded were analysed for abundance, density, frequency, index diversity, and index evenness.

Basal Area and Relative Basal Area (Hanson and Churchill, 1961)

Basal area (sq. cm) = $\frac{\pi \times (\text{dbh})^2}{4}$ and

Relative basal area (%) = $\frac{Basal\ area\ of\ species\ A}{Total\ basal\ area\ of\ all\ species} \times 100$,
where π = 3.14.

Dominance Index (C) (Simpson, 1949)

To assess the dominance within the community, the dominance index was calculated as follows:

$$C = \sum (ni/N)^2,$$

where ni is the IVI for each species, and N represents the total IVI of all species.

Margalef's Richness Index (R_1) (Margalef, 1958)

Margalef's Richness Index was calculated as

$$R_1 = \frac{S-1}{ln(n)},$$

where S represents the total number of species and n represents the total number of individuals observed in the community.

Shannon's Index or α Diversity (H') (Shannon and Weaver, 1963)

The diversity index was determined using the Shannon–Wiener diversity index method:

$$(H') = H' = -\sum_{i=1}^{S} (pi \log_2 pi) \text{ or } H' = -\sum_{i=1}^{S} (ni/n) \log_2 (ni/n),$$

where pi represents the proportion of the total sample belonging to a specific species, pi's represents the population parameters, $\log_2$ is equivalent to 3.322 $\log_{10}$, ni refers to the number of individuals of species i in the sample, and n represents the total number of all species.

Evenness Index (E) (Hill, 1973)

The evenness index was calculated as

$$E = \frac{1/(1/\lambda)}{e^{H'} - 1} \text{ or } E = \frac{N_2 - 1}{N_1 - 1},$$

where H' refers to Shannon's index, λ refers to Simpson's index, and N_1 and N_2 represent Hill's diversity numbers.

Ecological parameters

The following ecological parameters were measured: topographic, microclimatic, and edaphic factors. Topographic factors included altitude and slope, while microclimatic factors included rainfall, temperature, and relative humidity. Edaphic factors included the following chemical properties of soil: CEC; P, Potassium (K), Calcium (Ca), and Magnesium (Mg) concentrations; and N total. The slope was measured using a clinometer.

Microclimatic parameters

Temperature, wind speed, light intensity, and humidity were measured using a portable gauge (Lutron LM-8010) and a data logger (Benetech GM 1365) at each plot. Rainfall data for the Cibodas Biosphere Reserve area from 2010 to 2021 (Figure 1) were obtained from secondary sources using the website https://power.larc.nasa.gov/.

Edaphic parameters

To assess edaphic parameters, 24 soil samples were collected from the four locations. A modified version of the soil sampling method proposed by Zhang et al. (2021) was used. Topsoil samples were collected using a cylinder core to extract the topsoil layer at a depth of 0–15 cm or horizons O and A. The collected samples were weighed, recorded, and analysed. The analysis covered soil nutrients, including Ca, Mg, K, % C, % N, and % P, and CEC, following the protocol suggested by Huluka and Miller (2014). The analysis was conducted at the Pusat Penelitian Tanah dan Agriklimat (Research Centre for Soil Research and Agroclimate) and the Indonesian Center for Biodiversity and Biotechnology (ICBB) Laboratory, PT Biodiversitas Bioteknologi Indonesia, Bogor. Additionally, soil pH was measured directly in the field using a pH meter and soil tester on soil samples collected from each location.

Canonical correspondence analysis

Analysis of the impact of environmental factors, which comprised edaphic and microclimatic factors, on the distribution of types was carried out with ordination analysis techniques. This technique is widely used in the study of modern ecology (Li et al., 2017). Ordination techniques provide an objective representation to determine the relationship between environmental factors and type distribution. In the ordination diagram, the nature of the relationships is shown by vectors, with lengths being proportional to their importance and directions indicating their correlations with each axis. Canonical correspondence analysis (CCA) was conducted using PAST version 4. The basal area and environmental data were transformed using log (x+1) to consider zero values and prevent high values from influencing the ordination (Aissat, 2023). The basal area of the tree stage was used for CCA across all locations.

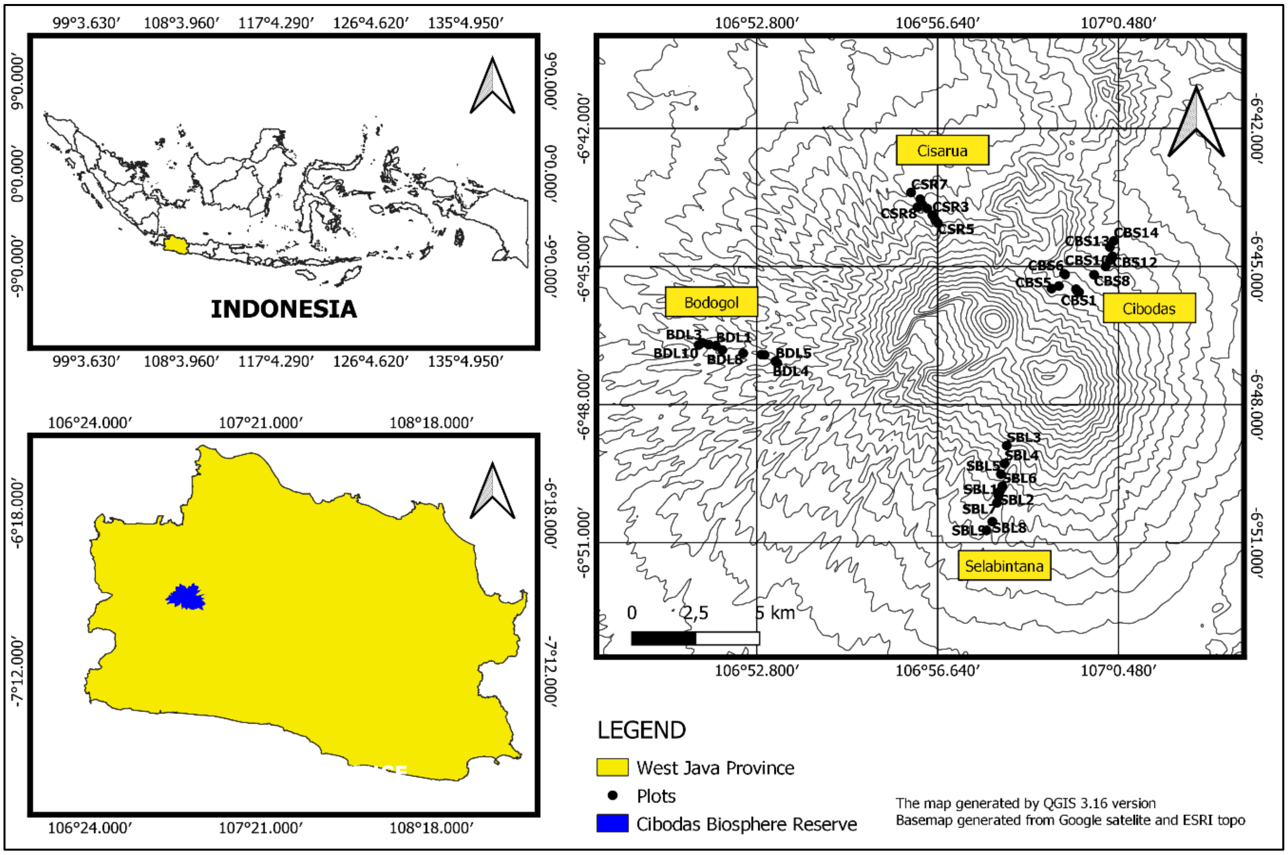

Figure 1. Study area in Cibodas Biosphere Reserve, West Java, Indonesia.

RESULTS

Forest structure

The vegetation analysis of floristic composition of the study site resulted in 155 species (Table 1). Based on basal area, the families Fagaceae, Theaceae, Euphorbiaceae, Elaeocarpaceae, Proteaceae, Araliaceae, Rhamnaceae, Anacardiaceae, Podocarpaceae, and Altingiaceae were found to be the most common in the study area, and *S. wallichii* was found to have the highest basal area. The results of the vegetation pattern analysis across the four different locations with an altitudinal range of ca. 750–1800 m asl are presented in Table 2. The tree stage had the highest number of species, while the pole stage had the lowest. The diversity index was relatively high for all stages.

Table 2 demonstrates that the forest in the Cibodas Biosphere Reserve, located at an altitudinal range of ca. 750–1800 m asl, has high diversity. However, based on the evenness index value (less than 1), it can be concluded that the distribution of species in the area is uneven. The vegetation structure of the lower stages was found to differ in composition from the higher stages (wilding to tree stages). These differences could be attributed to competition and predation factors in the study area. Regarding the dominant species composition in the forest, especially for the pole and sapling stages, invasive species, namely *Cestrum aurantiacum* and *Chinchona pubescens*, tended to dominate the area. This is inseparable from the existence of natural forests with quinine plantations and the Cibodas Botanical Garden, as examined by Zuhri and Mutaqien (2013) regarding the possibility for plant collections to escape from botanical gardens and become exotic in natural forest areas, such as *Cestrum aurantiacum*, *Calliandra calothyrsus*, and *Cinchona pubescens*. Consequently, in the long term, this can affect the survival of endemic species and change the natural vegetation structure of the Gunung Gede Pangrango forest.

All zones covered in the study represent the distribution range of *Castanopsis.* Most *Castanopsis* species were found across all altitudes, except *C. tungurrut, Castanopsis acuminatissima*, and *C. argentea*, which were distributed at elevations.

Table 1. The floristic composition of the four sampling locations. BA is the basal area derived from the diameter at breast height. Dominant species are indicated by an asterisk (*).

		Cibodas	Bodogol	Selabintana	Cisarua
Number of plots		14	10	9	8
Number of species		72	83	54	47
Plot size					
Species	**Family**				
Acer laurinum	Sapindaceae	0.214		0.005	
Acronychia pedunculata	Rutaceae	0.467	0.056	0.352	
Acronychia trifoliolata	Rutaceaea		0.013		0.006
Agathis borneensis	Araucariaceae		0.004		
Aglaia sp.	Meliaceae		0.467		
Aglaia hiernii	Meliaceae		0.115		
Alangium chinense	Cornaceae	0.019			
Alangium rotundifolium	Cornaceae			0.017	0.381
Albizia sp.	Fabaceae			0.009	
Altingia excelsa	Altingiaceae	4.473*	0.201	0.074	
Antidesma tetrandrum	Phyllanthaceae	0.012			0.033
Archidendron clypearia	Leguminosae		0.183		
Artocarpus elasticus	Moraceae		0.136		
Bonnetia sp.	Bonnetiaceae				0.028
Brassaiopsis glomerulata	Araliaceae	0.041			
Bridelia insulana	Phyllanthaceae	0.056	0.030		
Brugmansia suaveolens	Solanaceae			0.003	
Calliandra calothyrsus	Fabaceae		0.044		
Caryota mitis	Arecaceae				0.079
Casearia coriacea	Salicaceae		0.118		0.120
Castanopsis argentea	Fagaceae	4.881*	0.030		0.275
Castanopsis javanica	Fagaceae	3.478*	0.276	0.376*	0.996*
Castanopsis tungurrut	Fagaceae	1.066	1.125*	0.368	2.709*
Castanopsis acuminatissima	Fagaceae				0.707*
Celtis sinensis	Cannabaceae				0.006
Cestrum aurantiacum	Solanaceae	0.185			
Cinchona pubescens	Rubiaceae			0.026	0.129
Cinnamomum rhynchophyllum	Lauraceae		0.093		
Claoxylon longifolium	Euphorbiaceae		0.005		
Coffea sp.	Rubiaceae			0.006	
Coprosma sp.	Rubiaceae		0.002		
Croton argyratus	Euphorbiaceae		0.010		
Cryptocarya ferrea	Lauraceae	0.011	0.017		
Cryptocarya laevigata	Lauraceae		0.096		
Dacrycarpus imbricatus	Podocarpaceae	4.232*	0.007		
Daphne composita	Thymelaeaceae			0.045	
Decaspermum fruticosum	Myrtaceae	0.019			
Dendrocnide stimulans	Urticaceae	0.008			0.010
Dipterocarpus hasseltii	Dipterocarpaceae		0.140		
Dysoxylum alliaceum	Meliaceae	0.036		0.121	
Dysoxylum nutans	Meliaceae		0.062		
Dysoxylum parasiticum	Meliaceae		0.152		
Dysoxylum excelsum	Meliaceae		0.068	0.003	
Ehretia javanica	Boraginaceae				0.006
Elaeagnus latifolia	Elaeagnaceae	0.004			
Elaeocarpus acronodia	Elaeocarpaceae	0.142	0.070	0.158	
Elaeocarpus petiolatus	Elaeocarpaceae			0.400	
Elaeocarpus sp.	Elaeocarpaceae		0.132	0.188*	0.076
Elaeocarpus submonoceras	Elaeocarpaceae	0.047			0.046
Endiandra rubescens	Lauraceae		0.017		
Engelhardtia spicata	Juglandaceae	0.513	0.006		
Eriosolena composita	Thymelaeaceae	0.022			0.008
Euonymus indicus	Celastraceae		0.014		
Eurya acuminata	Pentaphylacaceae	0.034	0.037		0.014
Fagraea blumei	Gentianaceae	0.030			
Ficus alba	Moraceae	0.007	0.009		0.019
Ficus heterophylla	Moraceae	0.086		0.053	0.006
Ficus ribes	Moraceae	0.084	0.002	0.017	0.041
Ficus sp.	Moraceae		0.056	0.003	
Ficus variegata	Moraceae	0.016			

Ficus cuspidata	Moraceae	0.002			0.011
Ficus fistulosa	Moraceae		0.012		0.079
Ficus lepicarpa	Moraceae		0.066		
Ficus sinuata	Moraceae		0.004		
Flacourtia rukam	Salicaceae	0.003			
Garcinia forbesii	Clusiaceae		0.184		
Glochidion cyrtostylum	Phyllanthaceae	0.196		0.087	
Glochidion rubrum	Phyllanthaceae	0.003	0.008	0.030	
Gordonia excelsa	Theaceae	0.029	0.012		
Gynotroches axillaris	Rhizophoraceae				
Helicia robusta	Proteaceae		0.007		
Helicia serrata	Proteaceae	0.016	0.002	0.620*	
Itea macrophylla	Iteaceae			0.038	0.015
Itea sp.	Iteaceae			0.022	
Knema sp.	Myrysticaceae		0.065		
Laportea sp.	Urticaceae			0.031	
Lasianthus stercorarius	Rubiaceae			0.006	
Lindera polyantha	Lauraceae		0.310		
Lithocarpus elegans	Fagaceae	0.075	0.003	0.011	
Lithocarpus indutus	Fagaceae	0.028	0.148		0.016
Lithocarpus pseudomoluccus	Fagaceae	0.144	0.783*		0.004
Litsea resinosa	Lauraceae	0.004			
Litsea sp.	Lauraceae		0.019		
Litsea garciae	Lauraceae		0.169		
Litsea mappacea	Lauraceae				0.043
Macaranga rhizinoides	Euphorbiaceae	0.010	0.027	0.215	
Macaranga triloba	Euphorbiaceae			0.040	0.004
Macropanax concinnus	Araliaceae	0.781		0.278	
Macropanax dispermus	Araliaceae	0.530		0.397*	0.115
Maesopsis eminii	Rhamnaceae		0.931*		
Magnolia liliifera	Magnoliaceae	0.009			
Magnolia sumatrana	Magnoliaceae			0.367	
Magnolia montana	Magnoliaceae		0.009	0.027	0.024
Mallotus sp.	Euphorbiaceae		0.044		
Mangifera indica	Anacardiaceae		0.016		
Manglietia glauca	Magnoliaceae	0.261			0.275
Mastixia trichotoma	Cornaceae		0.004		
Melastoma	Melastomataceae			0.003	
Myristica sp.	Myristicaceae		0.055		
Myrtaceae	Myrtaceae			0.006	
Neolitsea cassiifolia	Lauraceae	0.197			
Neolitsea javanica	Lauraceae	0.137	0.044	0.309	
Neolitsea triplinervia	Lauraceae	0.273			
Neonauclea excelsa	Rubiaceae		0.002		
Neonauclea lanceolata	Rubiaceae		0.119	0.055	0.057
Orophea hexandra	Annonaceae			0.021	
Ostodes paniculata	Euphorbiaceae	0.258			0.407*
Pavetta montana	Rubiaceae				0.005
Persea excelsa	Lauraceae		0.158		
Persea rimosa	Lauraceae	0.655		0.095	0.060
Phoebe excelsa	Lauraceae	0.424	0.206		
Phoebe grandis	Lauraceae	0.083		0.007	0.016
Pinus merkusii	Pinaceae		0.025		
Piper sp.	Piperaceae			0.005	
Podocarpus neriifolius	Podocarpaceae	0.028		0.091	
Polyalthia subcordata	Annonaceae		0.003	0.001	
Polyathia sp.	Annonaceae		0.021		
Polyosma integrifolia	Escalloniaceae	0.055			
Prunus arborea	Rosaceae	0.183	0.409	0.251	
Pternandra azurea	Melastomataceae		0.031		
Rapanea hasseltii	Primulaceae	0.018			
Rauvolfia javanica	Apocynaceae				0.005
Rauvolfia sp.	Apocynaceae				0.089
Saurauia distatosa	Actinidiaceae	0.018			
Saurauia nudiflora	Actinidiaceae	0.005			
Saurauia pendula	Actinidiaceae	0.178			
Saurauia bracteosa	Actinidiaceae		0.029		
Schefflera aromatica	Araliaceae	0.149			

Schefflera sp.	Araliaceae	0.049			
Schima wallichii	Theacaea	6.131*	1.578*	2.554*	0.450*
Sloanea sigun	Elaeocarpaceae			0.089	0.035
Spondias pinnata	Anacardiaceae		0.529*		
Stemonurus secundiflorus	Stemonuraceae		0.002		
Sterculia sp.	Malvaceae		0.005		
Sterculia sp.	Malvaceae		0.184		
Sundacarpus amarus	Podocarpaceae		0.089		
Swietenia macrophylla	Meliaceae		0.113		
Symplocos cochinchinensis	Symplocaceae	0.011		0.019	0.004
Symplocos costata	Symplocaceae	0.057		0.011	
Symplocos fasciculata	Symplocaceae	0.004	0.005		
Syzygium antisepticum	Myrtaceae	0.144			
Syzygium densiflorum	Myrtaceae	0.021			
Syzygium nervosum	Myrtaceae	0.099			
Syzygium pycnanthum	Myrtaceae	0.071	0.020		
Syzygium rostratum	Myrtaceae	0.783	0.500		0.143
Syzygium sp.	Myrtaceae	0.047			
Syzygium racemosum	Myrtaceae		0.004	0.035	0.049
Turpinia sphaerocarpa	Staphyleaceae	0.356		0.101	0.078
Turpinia montana	Staphyleaceae		0.004		0.005
Vernonia arborea	Asteraceae	0.074		0.155	
Viburnum sambucinum	Adoxaceae			0.032	0.016
Villebrunea scabra	Urticaceae	0.427	0.056	0.296	0.296
Wendlandia densiflora	Rubiaceae		0.004		
Wenlandia sp.	Rubiaceae			0.146	
Wenmannia blumei	Cunoniaceae	0.025			

Plot size = 20 × 20 m.

Notably, *Castanopsis* diversity decreased with increasing altitude. This is a common phenomenon in which the number of species, species composition, structure, physiognomy, and tree architecture change as the elevation increases (Simbolon et al., 2012).

Factors influencing the distribution of Castanopsis

The ordination technique was used to assess the relationship between dominant trees and environmental factors (edaphic and climatic) (Figure 2). Environmental factors consisted of three climatic factors and six edaphic factors. *C. tungurrut* was found to be associated with moderate temperatures and lower altitudes; its distribution was more driven by increased temperature and decreased altitude than by edaphic factors. Other *Castanopsis* species recorded in this study, including *Castanopsis javanica*, *C. argentea*, and *C. acuminatissima*, showed variations in their relationship with environmental factors. *C. argentea* and *C. acuminatissima* were observed to be closely influenced by pH, while *C. javanica* was found to be more influenced by edaphic factors (N, K, P, and Ca concentrations, CEC, and pH) and altitude. Like *C. javanica*, *S. wallichii*, and *Dacrycarpus imbricatus* were likely more influenced by edaphic factors than by climatic conditions. The remaining species, including *Ostodes paniculate*, *Sloanea sigun*, *Cestrum aurantiacum*, and *Altingia excelsa*, were influenced by temperature and pH. Upon investigating the soil properties and microclimatic conditions, we observed variations in environmental factors at different elevations (Table 4).

DISCUSSION

Environmental factors influencing C. tungurrut and associated vegetation at Cibodas Biosphere Reserve

Table 1 presents variations observed in species composition per location, dominant species, and basal area values of *C. tungurrut* at the Cibodas Biosphere Reserve. The distribution of *C. tungurrut* and its correlation with environmental factors (edaphic and climatic factors) is illustrated in Figure 2. The edaphic and climatic factors covered in this study varied with altitudinal gradient (Table 4). Temperature tended to decrease with increasing altitude, while the edaphic factors, consisting of CEC and Mg, Ca, K, P, N, and C concentrations, varied at different altitudes. This variation could be attributed to the slope variation and decomposition rates per altitude. Additionally, the precipitation rate at the study site showed dry and wet months, with relatively high precipitation from December to March and lower precipitation in April (Figure 3).

C. tungurrut and nine dominant species were tested in relation to environmental variables using CCA (Figure 2). A total of nine environmental variables

Table 2. General characteristics of vegetation structure based on the density of species at various life stages at Cibodas Biosphere Reserve.

Scientific name	Life stage	Density	Total Number of Species	Diversity Index	Evenness Index
Schima wallichii Choisy	Tree	56.09	154	4.3	0.48
Villebrunea scabra (Blume) Wedd.	Tree	43.29			
Macropanax dispermus (Blume) Kunze	Tree	32.3			
Syzygium rostratum (Blume) DC.	Tree	31.09			
Castanopsis tungurrut (Blume) A. DC	Tree	23.17			
Macropanax concinnus Miq.	Tree	21.34			
Turpinia sphaerocarpa Hassk.	Tree	19.51			
Castanopsis javanica (Blume) A. DC	Tree	18.29			
Elaeocarpus sp	Tree	16.46			
Acronychia pedunculata (L.) Miq.	Tree	15.85			
Cestrum aurantiacum Lindl.	Pole	39	105	4.2	0.65
Lasianthus stercorarius Blume	Pole	36.5			
Polyalthia subcordata (Blume) Blume	Pole	36.5			
Turpinia sphaerocarpa Hassk.	Pole	31.7			
Syzygium rostratum (Blume) DC.	Pole	29.26			
Villebrunea scabra (Blume) Wedd.	Pole	26.8			
Cinchona pubescens Vahl	Pole	24.39			
Schima wallichii Choisy	Pole	24.39			
Macropanax undulatus (Wall.ex G. Donn) Seem	Pole	21.95			
Magnolia liliifera (L.) Baill.	Pole	21.95			
Lasianthus stercorarius Blume	Sapling	390	135	4.3	0.5
Cestrum aurantiacum Lindl.	Sapling	370			
Magnolia liliifera (L.) Baill.	Sapling	260			
Freycinetia insignis Blume	Sapling	230			
Polyalthia subcordata (Blume) Blume	Sapling	220			
Bartlettina sordida (Less.) R.M. King & H.Rob.	Sapling	200			
Psychotria montana Blume	Sapling	170			
Cinchona pubescens Vahl	Sapling	150			
Symplocos cochinchinensis (Lour.) S Moore	Sapling	150			
Acronychia pedunculata (L.) Miq.	Sapling	140			
Lasianthus laevigatus Blume	Wilding	3719.5	111	3.9	0.5
Elatostema strigosum Hassk.	Wilding	2560.9			
Psychotria montana Blume	Wilding	1707.3			
Cyrtandra picta Blume	Wilding	1158.5			
Trevesia sundaica Miq.	Wilding	1158.5			
Strobilanthes cernua Blume	Wilding	914.6			
Cestrum aurantiacum Lindl.	Wilding	853.6			
Piper baccatum C.DC.	Wilding	792.6			
Dichroa febrifuga Lour.	Wilding	731.7			
Ficus sp.	Wilding	731.7			

Table 3. Eigenvalues for axes of the ordination diagram.

Axis	1	2	3	4	5	6	7	8	9
Eigen value	0.5442	0.3127	0.1804	0.08146	0.05784	0.02982	0.02275	0.004598	1.28E-07

Table 4. Canonical coefficient and intra-set correlation of experimental variables with two axes of canonical correspondence analysis (CCA).

Axis variable	Canonical coefficient		Correlation coefficient	
	Axis 1	Axis 2	Axis 1	Axis 2
Slope	-0.16	-0.47	0.12	-0.54
CEC	-0.63	0.46	-0.68	0.42
C (%)	-0.5	0.47	-0.57	0.52
N (%)	-0.4	0.45	-0.56	0.52
K (cmol/kg)	-0.2	0.66	-0.43	0.3
Ca (cmol/kg)	-0.08	0.51	-0.36	0.36
Alt	-0.3	0.63	-0.31	0.71
Temp	0.5	-0.59	0.43	-0.54
pH	0.14	0.32	0.14	0.51

were analysed relative to 10 dominant tree species, resulting in nine axes, with a total variance of 44.1% and 25.5% for axis 1 and axis 2, respectively. The eigenvalues for axes 1 and 2 were 0.5542 and 0.3127, respectively. Based on the orthogonal projections, *C. tungurrut* is more likely to be found in areas with low pH, low Ca, low K, low altitude, low N, low C, low CEC, high temperature, and high slope. The species was found to have the strongest positive correlation with temperature (0.54) and a strong negative correlation with CEC (-0.49).

Based on the CCA ordination diagram (Figure 2), temperature can be defined as an important factor influencing the distribution of *C. tungurrut*. According to Körner et al. (2016), plants have well-defined threshold responses to temperature, which reveal unique abnormalities in cell function within a constrained temperature range, affecting the plant's survival, growth, and ability to regenerate. The result that temperature is the dominant climatic driver of *C. tungurrut* distribution conforms to the findings of previous studies by Harapan et al. (2022), Fathia et al. (2019), Kusmana and Suwandhi (2019), Santhyami et al. (2021), and Wibowo (2006). They revealed that temperature and altitude were the dominant factors influencing the distribution of *C. tungurrut* in Sumatera, while in West Java, including Mount Galunggung, Pakenjeng Garut and Mount Gede Pangrango, the altitude in the submontane zone (1000–1400 m asl) and slopes > 40% were observed to be the limiting environmental factors for the distribution of *C. tungurrut.* However, this finding is discordant with Paramita et al. (2022) and Sosilawaty et al. (2022), who found that *C. tungurrut can* also be found in peat swamp forests in Kalimantan, which had not been recorded before. Usually, *C. tungurrut* is found in lower to submontane forests. It is indicated that *C. tungurrut* can be tolerant of higher temperatures but is intolerant of lower temperatures, which are common at higher altitudes. In this regard, Schindlbacher et al. (2010) claimed that, compared to lower elevation locations, soil organic matter decomposition at higher elevation forests is more susceptible to climate change because it will be impacted in a more sensitive (cooler) temperature range.

On the other hand, a few dominant species found at the study site, including *C. javanica, C. argentea, S. wallichii, A. excelsa*, and *D. imbricatus*, were observed to be driven by edaphic factors rather than climatic factors. In this study, *C. javanica* was found to be more sensitive to lower C, Ca, N, and K content, CEC, pH, and altitude. In addition, *C. argentea and C. acuminatissima* were observed to be influenced by pH, while *O. paniculate and S. sigun* were found to be closely influenced by moderate to high temperatures.

Furthermore, previous studies by Hilwan and Irfani (2018), Putri (2021), and Wibowo (2006) on *C. argentea* have revealed different results indicating that the distribution of *C. argentea* is influenced by total N, altitude, CEC, temperature, and P content. In submontane forests and the surrounding forest (Telaga Warna Nature Reserve) in Java Mountain Forest, *C. argentea* dominated at 1100–1400 m asl and gradually diminished in number at higher elevations and at regions with higher P content. Wibowo (2006) found that *C. argentea* and other dominant species (*A. excelsa*, *Laportea stimulans, C. tungurrut*, and *C. javanica*) are not dependent on soil type, except *S. wallichii*.

Compared to other species found in this study, *C. tungurrut* was observed to be driven largely by temperature rather than edaphic factors, with a correlation of 0.54 ($p > 0.05$, not significant). Previous studies by Toledo et al. (2012) and Zhang et al. (2016) revealed that climatic factors are stronger drivers of species distribution in subtropical karst forests than edaphic factors. It is noteworthy that *C. tungurrut* can optimise soil nutrients, which enables the species to survive in nutrient-limited environments, exhibit tolerance to temperature changes, and form underground microbial associations, which have not been covered in this study.

Effect of environmental factors on C. tungurrut regeneration

The regeneration of *C. tungurrut* is correlated with environmental factors. It was found that edaphic and climatic factors contributed to the population and distribution of the species in its natural habitat (Table 2). We found that the tree stage of *C. tungurrut* was significantly influenced by temperature (Figure 2). The temperature gradient influenced the germination capacity and restoration of population in the natural habitat, as described in previous studies in semi-sunny slope habitats (Song et al., 2016; Zhao et al., 2021). In addition, temperature could shift the distribution of Fagaceae, as described in the distribution patterns of *Castanopsis echinocarpa* and *Castanopsis calathiformis* in tropical montane regions of Southwest China and *C. tungurrut* in Mount Geulis, West Java, in relation to their tolerance to low temperature and soil moisture (Du and Huang, 2008; Song et al., 2021; Lukman et al., 2022). Temperature

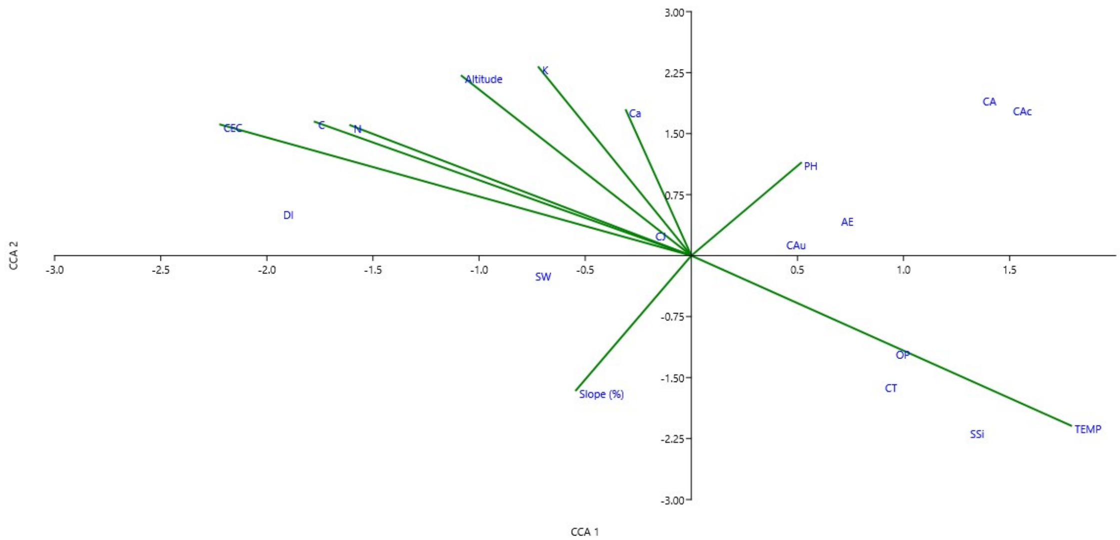

Figure 2. Ordination diagram of canonical correspondence analysis (CCA) showing *C. tungurrut* and nine selected dominant tree species with nine environmental variables (slope; CEC; C, N, K, and Ca concentrations; altitude; temperature; and pH). CT – *Castanopsis tungurrut*, CJ – *Castanopsis javanica*, CA – *Castanopsis argentea*, SW – *Schima wallichii*, AE – *Altingia excelsa*, DI – *Dacrycarpus imbricatus*, CAu – *Cestrum aurantiacum*, CAc – *Castanopsis acuminatissima*, OP – *Ostodes paniculata*, SSi – *Sloanea sigun*. The highest total variances of axis 1 and axis 2 are 44.1% and 25.5%, respectively. Total inertia is 1.2327462.

Table 5. Average values of environmental factors across various altitudinal gradients.

Altitude	Edaphic								Climatic		
	CEC	pH	P	N	C	Mg	Ca	K	Humidity	Slope (%)	Temp. (°C)
700–800	26,2	4.50	4.7	0.42	6.33	0.02	0.12	0.09	99.85	57.50	21.84
800–900	26.20	4.50	4.70	0.42	6.33	0.04	0.12	0.04	99.81	25.00	20.92
900—1000	31.44	5.40	3.15	0.67	11.36	0.03	0.12	0.05	99.97	35.50	20.40
1000–1100	40.72	5.00	3.00	0.84	14.10	0.02	0.06	0.03	99.92	44.50	19.10
1100–1200	28.62	6.23	16.83	0.83	13.80	2.32	14.13	1.07	95.23	17.33	19.33
1200–1300	39.41	5.73	15.07	1.28	20.25	1.51	5.43	0.18	99.54	45.00	18.09
1300–1400	42.86	5.93	45.41	0.95	16.83	0.39	187.09	35.55	99.87	24.40	18.34
1400–1500	28.65	5.98	13.99	0.93	14.39	0.51	8.96	8.45	99.67	18.86	17.59
1500–1600	41.29	6.00	19.74	1.55	26.75	0.84	133.78	25.39	99.92	19.00	16.99
1600–1700	62.88	5.20	41.80	2.20	42.23	0.23	175.38	84.83	99.94	25.20	16.12
1700–1800	42.20	6.15	56.91	1.29	25.00	0.19	83.31	40.25	99.84	27.50	15.70
S.D.	10.8	0.63	18.9	0.5	10.3	0.7	75.6	27	1.3	13	1.9

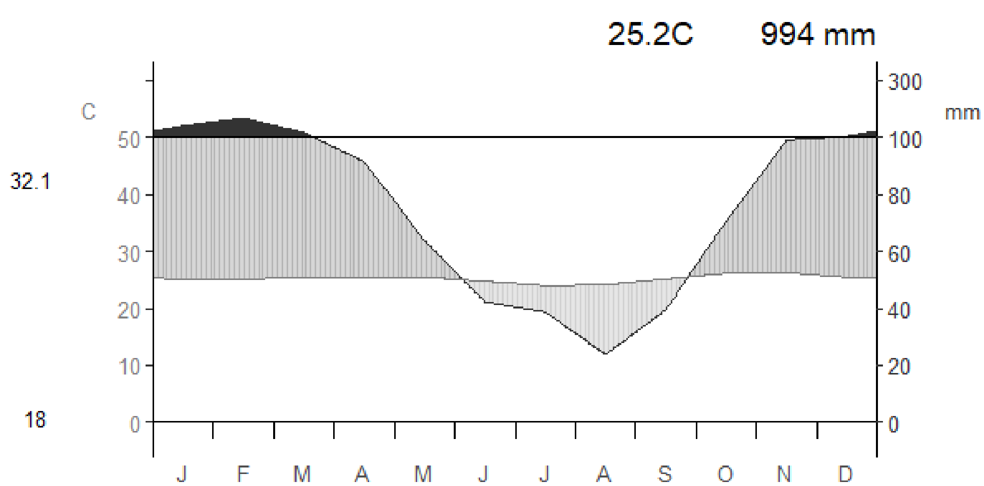

Figure 3. Monthly precipitation average in Gede Pangrango National Park, Cibodas Biosphere Reserve, Indonesia, during 2010–2021.

is considered as a predominant factor in the distribution of C. *tungurrut* because nutrient availability is closely related to slope declivity and temperature. Nutrient availability and temperature tend to decrease with increasing altitude, contributing to soil decomposition.

CONCLUSION

The distribution of *C. tungurrut* is driven largely by temperature rather than edaphic conditions (macronutrients). The tree stage of *C. tungurrut* tends to distribute at higher altitudes (1500 m asl), with temperatures around 16˚C as the lowest temperature limit, and can tolerate higher temperatures at lower elevations. Environmental factors significantly affect the distribution pattern of *C. tungurrut*. The species is well adapted to low soil nutrition in warm temperatures. However, the selected dominant species in the study area responded differently to environmental factors. Most dominant species were more significantly impacted by edaphic factors than by climatic factors.

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