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RESEARCH ARTICLE

Population ecology, phenotypic variation and conservation strategy of wild banana *Musa acuminata* Colla: a case study in Bromo Tengger Semeru National Park, East Java, Indonesia

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Abstract *Musa acuminata* is a major wild banana species close-relative to modern bananas. It provides important genetic materials for further banana improvement to address global threats. However, the population ecology, phenotypic variation, and conservation strategies of wild bananas in Indonesia remain poorly understood. This current study, located at Bromo Tengger Semeru National Park (BTSNP) in East Java as a showcase, revealed that wild banana *M. acuminata* populations were abundantly distributed in clumped patterns on open areas with high light intensities and air humidities from lowland to submontane and montane zones. The population structures were considered healthy and sustainable; dominated by juvenile and mature-vegetative, followed by suckers and a small proportion of mature-generative. The communities were found to be more abundant and had higher phenotypic richness at elevations above 1300 m asl than at lower elevations. Environmental conditions, particularly the light intensity, land slope and soil properties, are factors that contribute significantly to the ecology of wild banana populations. Based on phenotypic characterisation, it was identified as a complex variety of *M. acuminata* var. *rutilifes*, *nakaii* and *zebrina*. *M. acuminata* var. *rutilifes* mostly occupied lower elevations, while var. *nakaii* and/or *zebrina* at higher elevations. Phenotypic differentiation was significantly related to elevation as one of the geographical barriers. Based on the SWOT analysis, the suitable conservation strategy for wild banana in BTSNP is assertive or proactive. In-situ, ex-situ and on-farm conservation approaches are suggested. Bioprospecting research on wild bananas is encouraged. Due to the lack of public knowledge about the importance of wild banana conservation, awareness raising is also prioritised as a conservation action.

Keywords Conservation · Habitat · Morphology · *Musa acuminata* · Population

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Introduction

Wild banana is one of the plant genetic resources belonging to the genus *Musa* that is widely spread in Indo-Malesia to the Pacific regions (De Langhe et al. 2009). There are approximately 70 described species of *Musa* (Hakkinen, 2013), of which about 11–13 species are found in Indonesia. Wild bananas are known as the wild relatives of modern bananas. The origin of many cultivated bananas is mainly attributed to two species, *Musa acuminata* Colla and *M. balbisiana* Colla, which contributed through intra and interspecific hybridisation (Ortiz 2011). No less than a thousand cultivated varieties (cultivars) of bananas are formed and distributed throughout the tropics and subtropics (Perrier et al. 2011). In Indonesia, more than 200 cultivars are recognised (Hapsari et al. 2018), and some of them have become a vital commodity with a production value reaching 8.74 million tonnes in 2021 (Central Agency on Statistic RI 2021).

Compared to their wild relatives, cultivated bananas are considered more susceptible to various global challenges, both biotic and abiotic stresses due to the changing climate such as heat, drought, salinity stress, flooding, pest and disease outbreaks (Müller et al. 2021; Eckardt et al. 2023). Some of the current major diseases threats to banana plantations include *Fusarium* wilt, blood disease, banana bunchy top virus, yellow and black Sigatoka, *Xanthomonas* wilt, etc. (Drenth and Kema 2021). Their wild relatives often contain higher genetic diversity and essential traits for agriculture that might be lost in cultivars during domestication (Ortiz 2011; Hajjar and Hodgkin 2007). Such important genetic materials are useful for further banana breeding to better cope with environmental stresses, pests, and diseases, as well as to enhance important agronomic features, including yield, quality, and morphological traits (Dempewolf et al. 2017).

As the origin center and diversity, Southeast Asia, including Indonesia's tropical rainforests, becomes a suitable habitat for wild bananas (Mertens et al. 2021a; Vu et al. 2023). Specifically, *M. acuminata* species grows best in warm areas and open places with adequate moisture and tends to be most abundant on slopes (Nasution 1991). *M. acuminata*, as previously known about wild bananas, is considered as herbaceous pioneer plant in forest succession. It is recognized to colonise and dominate disturbed sites of the forests (Kallow et al. 2020). However, the habitats of wild banana populations are under considerable risk due to both natural and anthropogenic threats, such as forest fires, forest fragmentation, forest conversion, illegal logging, foraging, etc. The Ministry of Environment and Forestry (2022) reported that Indonesia had lost around 115,459 hectares of forest cover in 2020. Thus, the design and implementation of conservation strategies for wild bananas are required, particularly for *M. acuminata* as one of the major progenitors of modern bananas. This will ensure the steady maintenance of these important genetic resources and prevent them from becoming extinct, allowing their further utilisation.

The wild banana *M. acuminata* exhibites high phenotypic and genetic variation at infraspecific level. Several opinions about its division at the infraspecies level are still being debated. It is diverged into seven subspecies based on the morphological differences and geographical distribution (Perrier et al. 2011), i.e. subsp. *acuminata*, *errans*, *halabanensis*, *malaccensis*, *microcarpa*, *siamea*, and *truncata*. Meanwhile, Nasution (1991) divided *M. acuminata* into 15 varieties based on their morphological characteristics, i.e. var. *alasensis*, *halabanensis*, *acuminata*, *flava*, *tomentosa*, *sumatrana*, *nakaii*, *zebrina*, *bantamensis*, *breviformis*, *cerifera*, *longepetiolata*, *malaccensis*, *microcarpa*, and *rutilifes*. Generally, *M. acuminata* is characterised as a herbaceous perennial with slender pseudostem, large blotches at the petiole base, simple and broad leaves, seeded fruits, horizontal to pendulous inflorescence, and fruit straight to curved with smooth peel. Nonetheless, this species has varying features in leaf blade, petiole margins, male bud, female flowers, male flowers, rachis, and fruits (Nasution 1991; Javed et al. 2002; Hapsari 2014). Hence, its highly varied and overlapping morphological characteristics make them difficult to precisely identify until the infraspecific level.

Limited information is available regarding the population ecology of the wild banana *M. acuminata* in Indonesia. Population ecology is the discipline that investigates the dynamics of species populations and how these populations interact with the environment. Furthermore, population ecologists seek to understand the spatial and temporal patterns in the abundance and distribution of organisms, as well as the mechanisms that generate these patterns (Griffith et al. 2016). The multivariate aspects of population ecology provide researchers and related stakeholders with a better understanding of how organisms interact and facilitate species management, conservation, and protection strategies (Snider and Brimlow 2013).

Hence, this study aimed to investigate the population ecology of the wild banana *M. acuminata* in Bromo Tengger Semeru National Park (BTSNP), East Java, Indonesia as a case study. The rainforest of BTSNP provides an excellent model of wild *M. acuminata* habitat. The forest ecosystem consists of lowland, submontane, montane and subalpine. Thus, the populations were grouped based on the elevation difference of the sampling points as a geographical barrier. In addition, this study also aimed to reveal the species identity and phenotypic variation between and within populations. Eventually, from the study results, we construct and propose a recommendation for the conservation strategy of wild *M. acuminata,* specifically in BTSNP, and hopefully can be adopted to broader implementation in the tropical forests of Indonesia and Southeast Asia where wild *M. acuminata* is native.

Materials and methods

Study site

The fieldwork was conducted in the in-situ conservation area of Bromo Tengger Semeru National Park (BTSNP) during the rainy season from October to November 2020. BTSNP is one of the national parks in East Java, Indonesia. It is geographically located at S 7°54′–8°13′ and E 112°51′–113°04′ with an elevation range of 750–3676 m above sea level (asl) (Fig. 1). The total extent of BTSNP is approximately 50,276.2 Ha and administratively under four regencies, i.e. Lumajang (23,340.35 Ha), Malang (18,692.96 Ha), Pasuruan (4642.52 Ha) and Probolinggo (3600.37 Ha) (BTSNP 2023).

The forest ecosystems in BTSNP are classified into four types according to the elevation and air temperature differences, consisting of lowland, submontane, montane and subalpine; with the richness of flora around 1250 species (Hidayat and Risna 2007; BTSNP 2023). According to the climate classification

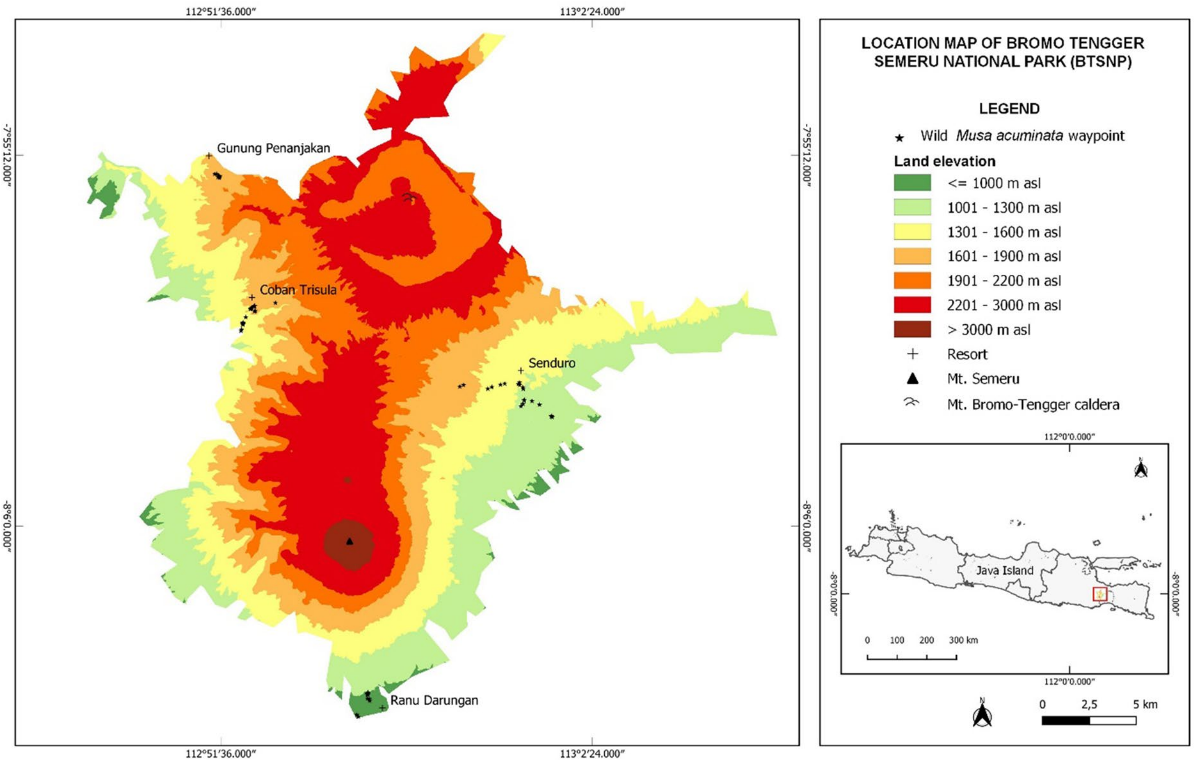


Fig. 1 Study site of wild banana *M. acuminata* populations in BTSNP, East Java, Indonesia

of Schmidt and Ferguson, BTSNP is categorised as type A in the southern part and type B in the north with air temperature ranges of 5°–22 °C, air relative humidity ranges of 42–97%, average annual precipitation ranges of 3000–6600 mm/year and air pressure ranges of 1007–1015.7 mm Hg (Ministry of Forestry RI, SK No. 278/Kpts-VI/97).

The BTSNP comprises 12 resorts (RPTN) under four management territories (SPTN I–IV). Each resort is divided into several zones, i.e. core zone, jungle zone, utilisation zone, rehabilitation zone, and special zone (BTSNP 2023). In this study, four resorts were selected as study sites for observing wild banana populations representing each management territory, i.e. Gunung Penanjakan Resort (SPTN I, Pasuruan), Coban Trisula Resort (SPTN II, Malang), Senduro Resort (SPTN III, Lumajang) and Ranu Darungan Resort (SPTN IV, Lumajang) (Fig. 1).

Method for sampling and population structure of wild banana *M. acuminata*

The sampling was conducted using a focused survey method (Brewer 2013), focusing on areas with high potential habitats for the wild banana *M. acuminata* clumps in four selected resorts. To collect data on the stage structure and identify the population structure of the wild banana community, a modified vegetation analysis was employed by establishing quadrat observation plots with a size of 20 m × 20 m. The plant stage structure was classified into four classes, i.e. (1) sucker, (2) juvenile, (3) mature-vegetative (not fruiting), and (4) mature-generative (flowering and fruiting) (Fig. 2). The number of individuals at each stage of survey intensity was recorded within the plot.

A total of 61 sampling plots were established. For the study of phenotypic variation, a purposive sampling method was employed. About 37 mature-generative individuals with complete characters were selected for detailed phenotypic characterisation. Furthermore, the wild banana sampling points were differentiated representing 4 groups of elevations, i.e. (1) ≤ 1000 m asl, (2) 1001–1300 asl, (3) 1301–1600 m asl, and (4) 1601–1900 m asl. Wild banana samples from the same elevation group were treated as the same population (Table 1 and Fig. 1).

Measurement of habitat and ecological characteristics

Habitat and ecological characteristics, consisting of microclimatic factors and soil characteristics, were recorded on the sampling plots. Microclimatic factors were observed including real-time average air temperature and relative humidity using a thermohygrometer (Dekko 642N), the sunlight intensity using a lux meter (LX-1102), and the pH and soil moisture using a soil tester (Takemura DM-5). The geographical position and elevation were recorded using a GPS (Garmin Map 62sc), and the land slope was measured using a clinometer (Suunto PM-5). To carry out a conservation strategy analysis, the components of strengths, weaknesses, opportunities, and threats to the habitat and wild banana populations in BTSNP were noted.

Fig. 2 Plant stage structure of wild banana

Table 1 Population sample list of mature-generative individuals of wild banana *Musa acuminata* for complete phenotypic characterisation

No	Code	Regional Station			Land slope (°)	Elevation (m asl)	Population by elevation (m asl)
		SPTN	RPTN	Regency			
1	1–1	IV	Ranu Darungan	Lumajang	31–45	987	Pop. 1 ≤ 1000 (Lowland)
2	1–2	IV	Ranu Darungan	Lumajang	31–45	973	
3	1–3	IV	Ranu Darungan	Lumajang	15–30	971	
4	1–4	IV	Ranu Darungan	Lumajang	6–15	935	
5	1–5	IV	Ranu Darungan	Lumajang	6–15	928	
6	1–6	IV	Ranu Darungan	Lumajang	6–15	852	
7	1–7	IV	Ranu Darungan	Lumajang	6–15	842	
8	2–1	III	Senduro	Lumajang	16–30	1287	Pop. 2 1001–1300 (Submontane)
9	2–2	III	Senduro	Lumajang	0–5	1262	
10	2–3	III	Senduro	Lumajang	0–5	1262	
11	2–4	III	Senduro	Lumajang	6–15	1252	
12	2–5	III	Senduro	Lumajang	0–5	1248	
13	2–6	III	Senduro	Lumajang	6–15	1234	
14	2–7	III	Senduro	Lumajang	6–15	1155	
15	2–8	III	Senduro	Lumajang	31–45	1130	
16	3–1	II	Coban Trisula	Malang	> 45	1586	Pop. 3 1301–1600 (Submontane)
17	3–2	III	Senduro	Lumajang	31–45	1540	
18	3–3	III	Senduro	Lumajang	> 45	1520	
19	3–4	II	Coban Trisula	Malang	> 45	1511	
20	3–5	II	Coban Trisula	Malang	> 45	1484	
21	3–6	II	Coban Trisula	Malang	> 45	1460	
22	3–7	II	Coban Trisula	Malang	> 45	1454	
23	3–8	III	Senduro	Lumajang	16–30	1439	
24	3–9	III	Senduro	Lumajang	> 45	1405	
25	3–10	III	Senduro	Lumajang	0–5	1348	
26	3–11	III	Senduro	Lumajang	0–5	1342	
27	3–12	III	Senduro	Lumajang	16–30	1312	
28	4–1	I	Gunung Penanjakan	Pasuruan	> 45	1753	Pop. 4 1601–1900 (Montane)
29	4–2	III	Senduro	Lumajang	> 45	1729	
30	4–3	I	Gunung Penanjakan	Pasuruan	> 45	1714	
31	4–4	I	Gunung Penanjakan	Pasuruan	> 45	1704	
32	4–5	III	Senduro	Lumajang	> 45	1703	
33	4–6	II	Coban Trisula	Malang	> 45	1668	
34	4–7	I	Gunung Penanjakan	Pasuruan	> 45	1663	
35	4–8	II	Coban Trisula	Malang	> 45	1657	
36	4–9	I	Gunung Penanjakan	Pasuruan	> 45	1629	
37	4–10	II	Coban Trisula	Malang	> 45	1623	

For further soil analysis, the disturbed soil samples were collected at a depth of 0–10 cm, with 3 replications per population. The soil analysis was conducted at the Soil Laboratory, Faculty of Agriculture, Brawijaya University, Malang, East Java, Indonesia. The soil chemical properties analysed consisted of pH value (pH H_2O), organic C (Walky and Black method), total N (Kjeldahl method), C/N ratio, P (Bray 1 method), exchangeable cations (K-Na-Ca-Mg) and cation exchange capacity (CEC) (extraction method using

NH4OAc 1 N pH 7). Total bases are the sum of the K, Mg, Ca, and Na. Base saturation is calculated as the percentage of CEC occupied by base cations. In addition, soil texture was analysed using the pipette method.

Plant materials and method for phenotypic characterisation

Thirty-seven samples of mature-generative individuals were examined for phenotypic characterisation, representing four populations based on the elevation where the plots were taken (Table 1). The phenotypic observation and documentation were performed following the Descriptor for Banana from IPGRI-INIBAP/CIRAD (1996) with modifications. Each plant sample was characterised by recording 43 phenotypic traits, including both vegetative and generative organs, comprising 100 character states (Table 2). Furthermore, the description and identification of subspecies/variety of *M. acuminata* was referred to Nasution (1991).

Data analysis

The spatial distribution pattern of wild banana *M. acuminata* populations in BTSNP was analysed using the standardised Morisita index referred to Krebs (1998), as the following formula:

$$Id = n\frac{\left(\sum x_i^2 - \sum x_i\right)}{\left(\sum x_i\right)^2 - \sum x_i}$$

Id = Morisita index;

n = the total number of sampling plots;

x_i = the number of individuals in each plot.

If the value of Id ≤ 0, the similarity of the community is low; while Id ≥ 1, the similarity of the community is equal/high. Later, Mu and Mc was calculated using the following formula to determine the distribution pattern:

$$Mu = \frac{\chi^2_{0.975-n+\sum x_i}}{\left(\sum x_i\right) - 1}$$

$$Mc = \frac{\chi^2_{0.025-n+\sum x_i}}{\left(\sum x_i\right) - 1}$$

Mu = Morisita index for uniform pattern;

$X^2_{0,975}$ = value of Chi square table with n-1 free degree and confidence interval 97.5%;

Mc = Morisita index for clump pattern;

$X^2_{0,025}$ = value of Chi square table with n-1 free degree and confidence interval 2.5%

Then, the standard degree of Morisita was calculated by the formula:

$$Ip = 0.5 + 0.5\left(\frac{Id - Mc}{n - Mc}\right), \text{ If } Id \geq Mc > 1$$

$$Ip = 0.5\left(\frac{Id - 1}{Mc - 1}\right), \text{ If } Mc > Id \geq 1$$

$$Ip = -0.5\left(\frac{Id - 1}{Mu - 1}\right), \text{ If } 1 > Id > Mu$$

$$Ip = -0.5 + 0.5\left(\frac{Id - Mu}{Mu}\right), \text{ If } 1 > Mu > Id$$

The distribution pattern was concluded based on the Ip value, viz.:

a) $Ip = 0$, the individual plants are randomly distributed.
b) $Ip < 0$, the individual plants are uniformly distributed (regular).
c) $Ip > 0$, the individual plants are distributed in clusters (clumped).

The population structure was analysed based on population density at each plant stage referred to Odum (1998), as the following formula:

$$Dp = \frac{N}{A}$$

Dp = Population density.

N = number of individuals (population size).

A = area (unit^2).

Subsequently, the normality of population structure distribution was analysed using the Kolmogorov Smirnov test in SPSS 23.0 software.

The habitat of wild banana in BTSNP was described objectively based on the site characteristics data. Statistical tests were employed on environmental data using SPSS 23.0 software. The Tukey test was used to determine the significant difference with a 95% confidence level. The class

Table 2 Descriptor for wild banana phenotypic characterisation

No	Phenotypic character	Character state
1	Pseudostem height	1) < 5 m; 2) 5–7 m; 3) > 7 m
2	Pseudostem circumference	4) slender (20–40 cm); 5) medium (40–60 cm); 6) large (60–80 cm)
3	Pseudostem color	7) cream; 8) cream-green; 9) cream-red
4	Blotches at petiole base	10) sparse; 11) moderate; 12) extensive
5	Blotches color at petiole base	13) brown; 14) orange-brown; 15) brown-black
6	Petiole canal of the third leaf	16) erect; 17) spreading
7	Petiole margins winged	18) winged
8	Petiole margins clasping	19) not clasping
9	Petiole margins color	20) brown-black; 21) brown–red; 22) brown; 23) reddish-purple to red; 24) orange-brown
10	Edge of petiole margin	25) contrast
11	Color of midrib ventral surface	26) yellow-green; 27) reddish
12	Pigmentation of cigar leaf	28) green
13	Peduncle hairiness	29) hairless; 30) slightly hairy; 31) very hairy
14	Bunch position	32) slightly angle; 33) horizontal; 34) supra horizontal; 35) at 45° angle
15	Bunch shape	36) spiral; 37) asymmetric; 38) truncate; 39) cylindrical
16	Bunch appearance	40) lax; 41) compact
17	Male rachis position	42) with a curve; 43) falling vertically; 44) horizontal; 45) supra horizontal
18	Male rachis appearance	46) bare
19	Male bud shape	47) slender; 48) medium; 49) fat
21	Male bud length	50) short < 20 cm
22	Male bud shoulder	51) low; 52) medium; 53) high
23	Bract apex shape	54) pointed; 55) intermediate; 56) obtuse
24	Bract imbrication	57) convolute; 58) moderate
25	Bract behavior before falling	59) revolute; 60) not revolute
26	Bract external face color	61) orange-red; 62) red–purple; 63) purple
27	Bract internal face color	64) orange-red; 65) red-cream
28	Compound tepal main color	66) cream; 67) reddish
29	Lobe color	68) yellow
30	Anther color	69) cream-yellow; 70) reddish
31	Dominant color of male flower	71) yellowish-cream; 72) reddish
32	Number of hands per bunch	73) ≤ 5; 74) 5–10; 75) > 10
33	Number of fruit per hand (mid-hand)	76) ≤ 10; 77) 10–15; 78) ≥ 15
34	Fruit length at maturity	79) ≤ 10 cm; 80) 10–15 cm
35	Fruit shape (longitudinal)	81) slightly curved; 82) curved
36	Fruit apex	83) bottlenecked
37	Remains of flower relicts	84) without; 85) persistent
38	Fruit pedicel length	86) ≤ 10 mm; 87) > 10 mm
39	Fusion of pedicels	88) no visible; 89) partially
40	Fruit pedicel width	90) ≤ 10 mm; 91) > 10 mm
41	Pedicel surface	92) hairless; 93) hairy
42	Immature fruit peel color	94) green; 95) light green; 96) dark green; 97) yellowish green
43	Mature fruit peel color	98) light yellow; 99) yellow; 100) bright yellow

criteria for soil chemical properties referred to the Soil Research Institute (2009).

Principal component analysis (PCA) was conducted to construct a scatter biplot, the association pattern of wild banana community structure, and ecological factors between populations. The PCA was performed using Paleontological Statistics (PAST) ver. 4.04 software (Hammer et al. 2001) with multivariate ordination, correlation matrix, and between groups.

Phenotypic characterisation data was scored using a reference number of "0" or "1" to indicate the absence or presence of a character in the plant samples. All characters were treated as independent, unordered, and of equal weight. The binary matrix data were subjected to multivariate ordination PCA to construct a scatter biplot and showing the grouping pattern of phenotypic characteristics between populations. The PCA was employed using PAST ver. 4.04 software with variance–covariance matrix and between groups.

The parameters of phenotypic diversity were analysed using GenAlEx 6.5 software, a modified method for genetic diversity analysis (Peakall and Smouse 2012). The analysed parameters include the percentage of polymorphic phenotypic characters (P%), the average expected heterozygosity (He), and the Shannon information index (I). Furthermore, the distance matrix data was subjected to phenotypic variance analysis using GenAlEx 6.5 software, a modified method for the analysis of molecular variance (AMOVA). The analysis of phenotypic variance estimated and partitioned the total phenotypic variance of the populations and then tested the significance of partitioned variance components using non-parametric testing procedures with 999 permutations (Excoffier et al. 1992).

To construct the conservation strategy of wild bananas in BTSNP, an analysis of the strengths, weaknesses, opportunities and threats (SWOT) analysis was performed referring to Scolozzi et al. (2014). The SWOT analysis was carried out following four steps: 1) Deciding what to compare; 2) Identifying internal (strength and weakness) and external (opportunity and threats) key factors to build a hierarchical structure; 3) Calculating and normalising the performances to uniform the scales of the key factors; and 4) Calculating the SWOT coordinate values for internal and external assessment.

Results

Habitat and environmental characteristics

The habitats of wild banana *M. acuminata* populations in BTSNP examined in this study were found in all four resorts, i.e. Gunung Penanjakan, Coban Trisula, Senduro, and Ranu Darungan (Fig. 3). The elevation was ranged from 842 to 1782 m asl and divided into four groups. Wild banana samples from the same elevation groups were treated as the same

Fig. 3 The wild banana *Musa acuminata* communities in Bromo Tengger Semeru National Park (BTSNP): **a** Gunung Penanjakan (Resort I), **b** Coban Trisula (Resort II), **c** Senduro (Resort III), and **d** Ranu Darungan (Resort IV)

population. The land slopes varied from flat (0–5°) to very steep (> 45°). At lower elevations (populations 1 and 2), wild banana plants were commonly found on flat to moderate slopes, while at higher elevations (populations 3 and 4), they were found on steep to very steep slopes (Table 1).

In general, there were statistical differences in microclimatic and soil characteristics among the four habitats of wild banana populations, although some were insignificant, as shown in Table 3. Interestingly, the light intensities among habitat populations were considered high although not significantly different, on average ranging from 5252 to 28,991.5 lx. Whereas, the air temperature and humidity were significantly different, on average ranging from 23.48 to 27.45 °C, and 69.00% to 89.20%, respectively. Habitat populations at lower elevations tended to have higher light intensity, air temperature, and air humidity than those at higher elevations (Table 3).

Most of the soil chemical properties in the habitat of wild banana populations had significant differences, except for organic C and BS. Further, soil chemical contents at higher elevations tended to have higher average values than at lower elevations, except for the soil pH and P values. The mineral values of P, K, and Na at populations 2, 3, and 4 showed insignificant differences (Table 3). Meanwhile, the soil texture was categorised as loam in most wild banana population habitats with varying proportions of sand: silt: and clay. However, at population 4 (the highest elevation of 1601–1900 m asl), the soil texture had a significantly higher sand content than silt and clay, so it was identified as sandy clay loam soil (Table 3).

Table 3 Microclimatic and soil characteristics of the wild banana *Musa acuminata* population habitats in Bromo Tengger Semeru National Park(BTSNP). Data: means± standard deviations. The mean value followed by the same superscript letter in the same row shows nosignificant difference at the 95% confidence level with the Tukey test. Letter a is the highest significance valuefollowed by letters b and c

Environmental factors	Population by elevation (m asl)			
	Pop. 1 ≤ 1000	Pop. 2 1001–1300	Pop. 3 1301–1600	Pop. 4 1601–1900
Micro-climates				
Light intensity (lx)	28,991.50 ± 38,119.04^{a}	30,895.60 ± 70,783.30^{a}	7273.95 ± 15,371.80^{a}	5252.86 ± 6496.75^{a}
Avg. air temperature (°C)	26.88 ± 1.97^{a}	27.45 ± 2.79^{a}	23.80 ± 1.88^{b}	23.48 ± 2.20^{b}
Avg. air RH (%)	89.20 ± 8^{a}	69.00 ± 6.60^{b}	73.80 ± 9.32^{b}	75.00 ± 6.14^{b}
Chemical soil properties				
Soil pH	7.49 ± 0.17^{a}	7.29 ± 0.28^{ab}	7.14 ± 0.24^{b}	7.19 ± 0.33^{b}
Organic C (%)	3.78 ± 0.35^{a}	4.10 ± 1.03^{a}	3.56 ± 0.37^{a}	4.09 ± 0.38^{a}
N total (%)	0.37 ± 0.03^{b}	0.44 ± 0.08^{a}	0.38 ± 0.04^{b}	0.40 ± 0.03^{ab}
C/N ratio	10.00 ± 0.00 ^{ab}	9.30 ± 0.95^{bc}	9.15 ± 0.59^{c}	10.38 ± 0.86^{a}
P Bray 1 (mg/kg)	28.36 ± 6.64^{a}	11.14 ± 0.62^{b}	12.05 ± 2.43^{b}	15.34 ± 4.93^{b}
K (me/100 g)	0.22 ± 0.02^{b}	0.56 ± 0.12^{a}	0.54 ± 0.13^{a}	0.57 ± 0.21^{a}
Na (me/100 g)	0.17 ± 0.02^{b}	0.36 ± 0.03^{a}	0.36 ± 0.11^{a}	0.49 ± 0.24^{a}
Ca (me/100 g)	8.84 ± 1.03^{b}	9.80 ± 0.22^{ab}	9.97 ± 0.96^{ab}	10.80 ± 1.58^{a}
Mg (me/100 g)	0.57 ± 0.17^{b}	0.94 ± 0.22^{ab}	0.90 ± 1.02^{ab}	1.84 ± 1.37^{a}
CEC (me/100 g)	16.67 ± 0.005^{c}	20.27 ± 2.48^{b}	20.16 ± 2.30^{b}	23.48 ± 2.21^{a}
Total base (me/100 g)	9.79 ± 1.21^{b}	11.67 ± 0.23^{ab}	11.80 ± 2.06^{ab}	13.70 ± 3.21^{a}
BS (%)	58.50 ± 7.06^{a}	58.10 ± 6.74^{a}	58.40 ± 5.65^{a}	57.71 ± 9.56^{a}
Physical soil properties				
Sand (%)	45.30 ± 2.36^{b}	42.50 ± 3.81^{bc}	38.95 ± 4.42^{c}	49.48 ± 3.86^{a}
Silt (%)	42.30 ± 6.55^{a}	39.50 ± 3.34^{a}	41.80 ± 8.90^{a}	23.14 ± 5.06^{b}
Clay (%)	12.40 ± 5.13^{c}	18.00 ± 1.15^{b}	19.25 ± 4.96^{b}	27.38 ± 2.66^{a}
Texture	Loam	Loam	Loam	Sandy clay loam

Remarks: *CEC* cation exchange capacity, *BS* base saturation

Distribution pattern

To explain species-environment relationships based on species location data, including abundance and occurrence, the study of distribution patterns is crucial. Based on the standardised Morisita index calculations, all four populations of wild banana *M. acuminata* in BTSNP resulted in $Id \geq Mc > 1.0$ and $Ip > 0$. Thus, it can be concluded that the individual plants in all wild banana *M. acuminata* populations in BTSNP were distributed in clumps or clusters (Table 4).

Population structure

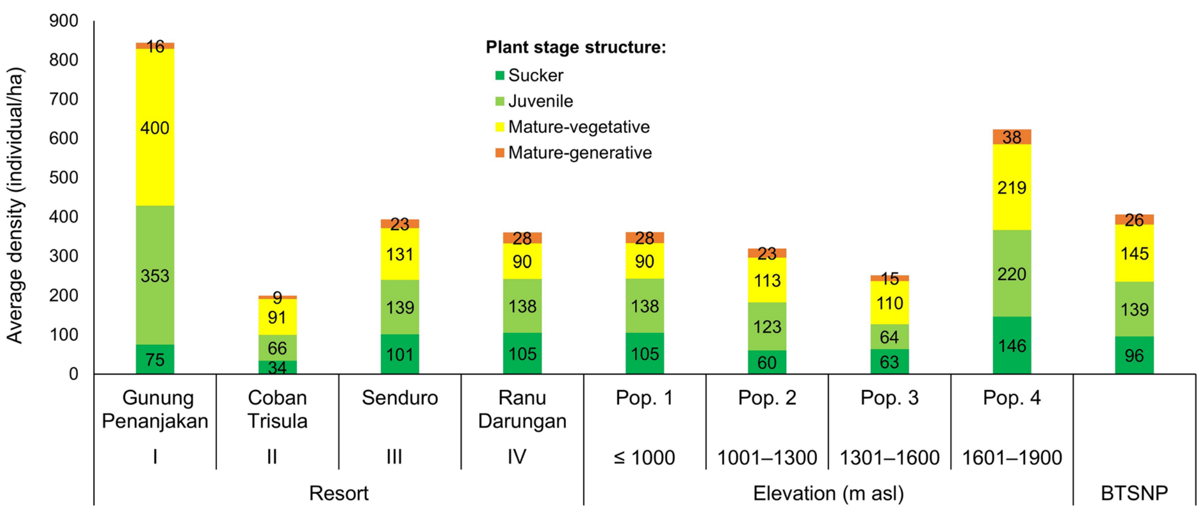
A total of 61 wild banana *M. acuminata* sampling plots were established during the fieldwork in BTSNP. About 996 individuals were recorded on the total extent of 24,400 m^2 of sampling plots, comprising 239 suckers, 340 juveniles, 353 mature-vegetative and 64 mature-generative. Analysis of population structure based on the resort showed that the largest population of wild banana *M. acuminata* was found at Gunung Penanjakan (Resort 1), followed by Senduro (Resort III), Ranu Darungan (Resort IV) and Coban Trisula (Resort II) (Fig. 4). The population of wild banana *M. acuminata* in Gunung Penanjakan was found to be at high elevation (1601–1900 m asl), whereas in Senduro and Coban Trisula was found spread at elevation of 1000–1300 m asl, and in Ranu Darungan at low elevation ≤ 1000 m asl (Table 2).

Thus, we concluded that the population structure is correlated with elevation, as a higher number of wild banana *M. acuminata* communities were found at elevations > 1300 m asl (populations 3 and 4), in contrast to lower elevations (populations 1 and 2). The population structure was mostly occupied by suckers, juveniles, and mature-vegetative plants in

Table 4 Distribution pattern of the wild banana *Musa acuminata* populations in Bromo Tengger Semeru National Park (BTSNP)

Population by elevation (m asl)	*Id*	*Mc*	*Ip*	Distribution pattern
Pop. 1 (≤ 1000)	1.9930	1.0701	0.5517	$Id \geq Mc > 1.0$ and $Ip > 0$, clumped
Pop. 2 (1001–1300)	1.2498	1.0795	0.5108	$Id \geq Mc > 1.0$ and $Ip > 0$, clumped
Pop. 3 (1301–1600)	1.2925	1.0693	0.5141	$Id \geq Mc > 1.0$ and $Ip > 0$, clumped
Pop. 4 (1601–1900)	3.3612	1.0271	0.6464	$Id \geq Mc > 1.0$ and $Ip > 0$, clumped

Remarks: *Id* Morisita index, *Mc* Morisita index for clump pattern, *Ip* standard degree of Morisita



Population structure of the wild banana *Musa acuminata* in Bromo Tengger Semeru National Park (BTSNP): average density (individual/ha) all populations. Whilst mature-generative plants were mostly found in population 4 (1601–1900 m asl) (Fig. 4).

The population structure of wild banana *M. acuminata* in BTSNP was dominated by juvenile (36.37%) and mature-vegetative plants (35.54%) with high average densities reaching 136 and 133 individuals per Ha, respectively. The suckers occupied about 26.20%, with an average density of 98 individuals per Ha. Only about 6.89% of the populations were flowering and fruiting (mature-generative), with an average density of 26 individuals per Ha (Fig. 4). Furthermore, the Kolmogorov–Smirnov test on the average density data showed a normal distribution at each plant stage in all populations.

PCA biplot of the population structure and habitat characteristics

The PCA of population structure data (abundance per plant stage) and twenty environmental variables resulted in three major principal components. The first two principal components of the PCA have eigenvalues of 13.72 and 6.78, respectively, contributing to a cumulative 85.42% of the total variance, as shown in Fig. 5. Furthermore, the PCA diagram showed that the habitat populations of wild banana *M. acuminata* were separated into three groups. Population 1 was clearly separated into group I. Population 2 was nested with population 3 in group II. Meanwhile, population 4 was separated into group III but intersected with population 3.

The PCA scatter biplot shown in Fig. 5 confirms that wild banana *M. acuminata* communities were abundant in the higher elevations (most of population 4 and part of population 3) and were strongly associated with soil properties. The mature-vegetative stage was influenced by the soil minerals, i.e. N, K, Ca, Na, and Mg, as well as other soil properties such as total base, C, CEC, and clay content of the soil. Likewise, the younger stages (sucker and juvenile) and mature-generative were related to the C/N ratio, soil texture, and sand content in the soil. Whilst, the microclimatic factors were strongly associated with the occurrence of wild bananas at the lower elevation (population 1).

Variation and PCA biplot of phenotypic characteristics

Phenotypic characterisation of 37 mature-generative individuals of wild banana *M. acuminata* in BTSNP reveals substantial variation in both vegetative and generative organs, as illustrated in Fig. 6. For instance, the petiole bases vary from green to reddish,

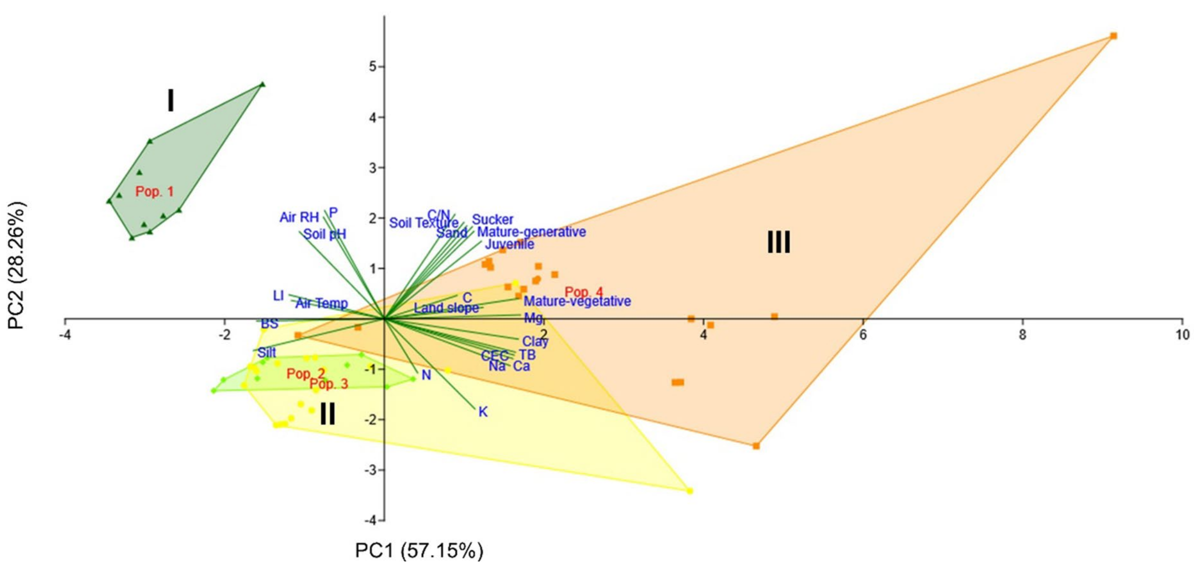


Fig. 5 Principal component analysis (PCA) scatter biplot of the wild banana *Musa acuminata* community structure and habitat characteristic between populations. Remarks: Pop. 1 (≤ 1000 m asl), Pop. 2 (1001–1300 m asl), Pop. 3 (1301–1600 m asl) and Pop. 4 (1601–1900 m asl)

Fig. 6 Phenotypic variation of the wild bananas *Musa acuminata* in Bromo Tengger Semeru National Park (BTSNP): **a** Petiole base reddish, with brown blotches, **b** Petiole base with brown-black blotches, **c** Petiole canal reddish, straight with erect margins, **d** Petiole canal green, open with spreading margins and green, **e** Male flowers dominant reddish, **f** Male flowers dominant yellowish-cream, **g** Color of the bract external face-purple and male bud shoulder-medium, **h** Color of the bract external face red purple and male bud shoulder-high, **i**–**k** Bunch shape asymmetric, compact, with curved fruits, and **l**–**n**. Bunch shape spiral, lax, with straight fruits

with brown to brown blotches. The petiole canals are straight with erect margins to open with spreading margins. The male flowers are mostly reddish to yellowish-cream. The bracts external faces are purple to red–purple, with medium to high shoulders. The bunchs are asymmetric to spiral, lax to compact appearances, with straight to curved fruits.

About 43 phenotypic characters were observed, consisting of 100 character states. The PCA of 100 phenotypic character states resulted in three major principal components. The first two principal components have eigenvalues of 2.02 and 1.34, respectively, contributing to a cumulative 78.29% of the total variance, as shown in Fig. 7. Furthermore, the wild banana *M. acuminata* populations in BTSNP based on phenotypic characters were separated into three groups. Populations 1 and 2 were separated as sisters in groups I and II, respectively. Whereas populations 3 and 4 were clustered together in group III.

The PCA scatter biplot in Fig. 7 showed that the phenotypic characteristics color of the bract external face—purple (63), anther color—cream yellow (69), and the dominant color of the male flower—yellowish-cream (72) highly contributed to the grouping of populations 1 and 2. These morphological features are typical characteristics of the species *M. acuminata* var. *rutilifes*. On the other hand, populations 3 and 4 were contributed by the color of the bract external face—red purple (62), anther color—reddish (70) and the dominant color of the male flower—reddish (71). These morphological features are typical characteristics of the species *M. acuminata* var. *nakaii* and *zebrina*.

It is suggested that samples of the wild banana populations of *M. acuminata* in BTSNP were identified as a complex variety of *M. acuminata* var. *rutilifes*, *nakaii*, and *zebrina*. Precise identification at the subspecies level is difficult due to overlapping characters between samples. Based on six key phenotypic characteristics from the PCA result (Fig. 7), the scientific identity proportion of wild banana *M. acuminata* varieties can be predicted (Fig. 8). Although imprecise, 20 out of the 37 samples observed were possibly identified as *M. acuminata* var. *rutilifes*, and the rest as var. *nakaii* or *zebrina*.

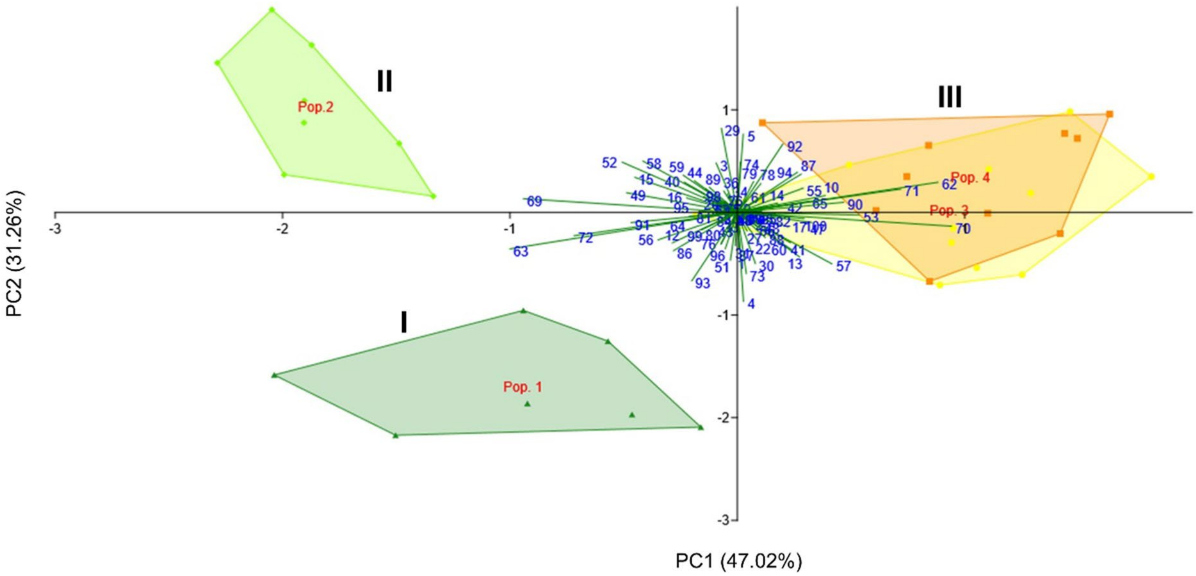


Fig. 7 Principal component analysis (PCA) scatter biplot of phenotypic characteristics among wild banana *Musa acuminata* populations in Bromo Tengger Semeru National Park (BTSNP). Remarks: Pop. 1 (≤1000 m asl), Pop. 2 (1001–1300 m asl), Pop. 3 (1301–1600 m asl), and Pop. 4 (1601–1900 m asl)

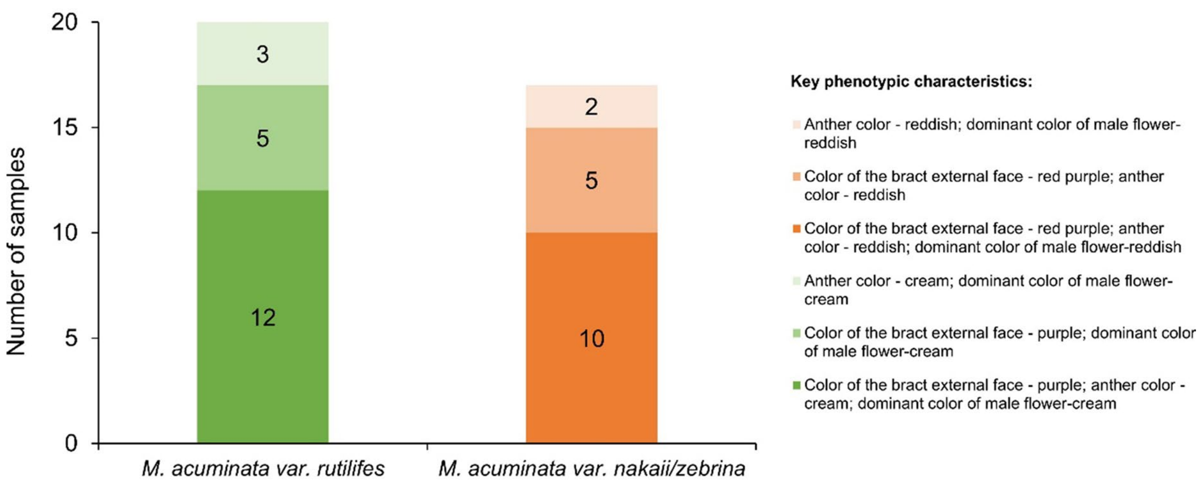


Fig. 8 Proportion of wild *Musa acuminata* varities based on key phenotypic characteristics from the principal component analysis

Phenotypic diversity among and within populations

Estimation of phenotypic diversity parameters, including the percentage of polymorphic phenotypic characters (P%), the average expected heterozygosity (He) and the Shannon information index, provides a measure of the taxa's phenotypic richness. This study detected a high phenotypic richness across wild banana *M. acuminata* populations in BTSNP, with an average polymorphic phenotypic character of 91.75%, a heterozygosity of 0.265, and a Shannon index of 0.467. Furthermore, the phenotypic diversity among and within populations revealed that population 3 had the highest phenotypic diversity (0.247), followed by population 4 (0.233), population 2 (0.208) and population 1 (0.199) (Fig. 9). Thus, we deduced that the heterozygosity of *M. acuminata* populations in BTSNP is high, which is in accordance to previous research in which a heterozygosity value of more than 0.20 for common plant families was considered as high (Hamrick and Godt 1996).

Analysis of the phenotypic variance of 37 samples of wild banana *M. acuminata* populations in BTSNP revealed that 85% of the variation was present within the populations and 15% of the variation was between the populations (Table 5). Furthermore, the PhiPT values can be used to infer the significance level of phenotypic differentiation of the populations. This present study resulted in a PhiPT value of 0.152, indicating a high genetic differentiation with the PhiPT values significant at 0.001 (Table 5). A PhiPT higher than 0.15 means the populations are significantly different (Frankham et al. 2002). The PhiPT value increases with the differentiation between populations (Nikmah et al. 2021).

SWOT analysis for conservation strategy

We utilized a SWOT analysis to develop and recommend an appropriate conservation strategy for wild bananas in BTSNP, based on data gathered from the field and the outcomes of this study. The internal factors of SWOT analysis consist of strengths (S) and weaknesses (W). The strength factor scores are high due to BTSNP being a nationally-protected area with high diversity and abundant populations of wild bananas and a suitable habitat and climate for their growth. Wild bananas are also easily propagated by suckers and seeds. However, some weaknesses were identified particularly a lack of priority for conservation and public knowledge of the important uses of wild bananas (Table 6).

The external factors of SWOT analysis consist of opportunities (O) and threats (T). The external factor with the highest impact on wild banana conservation is the opportunity for ex-situ conservation, such as Purwodadi Botanic Garden (PBG), through living collections and seed banks. Research on the diversity, conservation and bioprospecting of wild bananas is of increasing interest. In addition, there is also an opportunity to develop on-farm conservation of wild

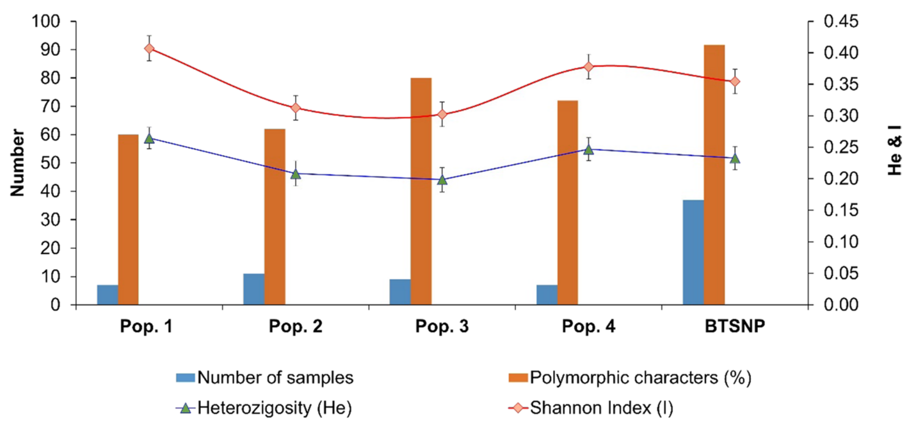


Fig. 9 Phenotypic diversity parameters of the wild banana *Musa acuminata* populations in Bromo Tengger Semeru National Park (BTSNP). Remarks: Pop. 1 (≤ 1000 m asl), Pop. 2 (1001–1,300 m asl), Pop. 3 (1301–1600 m asl), and Pop. 4 (1601–1900 m asl)

Table 5 Analysis of phenotypic variance of the wild banana *Musa acuminata* populations in Bromo Tengger Semeru National Park (BTSNP)

Variation source	Df	SS	MS	Est. Var	% P	PhiPT	Prob
Between populations	3	115.144	38.381	2.609	15	0.152	0.001
Within populations	33	481.558	14.593	14.593	85		
Total	36	596.703		17.202	100		

Remarks: *df* degrees of freedom, *SS* sum of squares, *MS* mean squares, *Est. Var*. estimated phenotypic variation, *% P* percentage of phenotypic variation, *PhiPT* phenotypic differentiation between populations, *Prob*. probability

Table 6 Internal factors analysis summary for conservation strategy of the wild bananas in Bromo Tengger Semeru National Park (BTSNP)

Internal factors	Weights	Rating	Score
Strengths (S)			
BTSNP is a national protected conservation area (in-situ)	0.11	4	0.44
There are at least three varieties of wild banana *Musa acuminata* in BTSNP i.e. *rutilifes*, *nakaii*, and *zebrina*. In addition, it has been reported that *M. balbisiana* and *Ensete glaucum* are also available	0.11	4	0.44
BTSNP contains a high phenotypic variation of wild banana *M. acuminata*. It provides important gene sources for further breeding of modern bananas: biotic and abiotic stress resistance genes	0.10	4	0.40
Habitat and climate in BTSNP are suitable for the growth of wild bananas	0.10	4	0.40
The population of wild bananas is known to be distributed in clumps at elevations of 800–1800 m asl	0.09	4	0.36
Wild bananas can be propagated through suckers and seeds, making it easy to obtain new individuals	0.05	2	0.10
Wild animals (primates, birds, bats, etc.) consume fruits and act as agents for seeds dispersal	0.05	1	0.05
Subtotal S	0.61		2.19
Weaknesses (W)			
Wild bananas have not been included in the list of priority flora protection by BTSNP and the government	0.10	4	0.40
Wild bananas have many seeds, so they are not edible and are considered economically useless by the community	0.10	4	0.40
Lack of public knowledge about the importance of wild bananas as genetic resources for banana breeding efforts	0.09	4	0.36
Lack of public knowledge about the benefits of wild bananas for functional food, health, cosmetics, etc	0.05	3	0.15
Lack of public knowledge regarding the identification of species/variety and phenotypic variations of wild bananas	0.05	3	0.15
Subtotal W	0.39		1.46
Total SW	1.00		3.65

bananas in particular regions near the BTSNP. Meanwhile, the main threat comes from human pressure in the form of land clearing, as wild bananas are considered weeds and harvested for miscellaneous uses (Table 7).

As shown in Tables 6 and 7, the total internal factor score was 3.65, with a higher score for S (2.19) than W (1.46). Whilst, the total external factor score was 3.65, with a higher score for O (1.92) than T (1.51). Furthermore, the calculation of the SWOT coordinate values for internal and external assessments resulted in the meeting point at quadrant 1 (S–O), indicating an assertive/proactive conservation strategy.

Discussions

Musa acuminata, a particular species of wild banana, is a perennial herbaceous plant widely found throughout Indonesia. It is preferable in open places with slightly moist soil, from lowland to mountainous areas (Nasution 1991). This current study showed that wild banana *M. acuminata* populations were abundantly distributed in clumps on open areas with high light intensities and air humidities in BTSNP, from lowland to montane areas (842 to 1782 m asl) (Table 1). The wild banana *M. acuminata* is commonly found from 10 to 1513 m asl in Indonesia (Hastuti et al. 2019). Meanwhile, Nasution (1991) reported that it is available up to 2000 m asl. The clumped distribution pattern of wild banana in BTSNP is obvious in nature, as it also corresponds to the growth type of the plant itself. The clumped distribution pattern is generally due to the way it reproduces offsprings, both vegetative or generative, that fall close to the parent (Wahyuni et al. 2017). In addition, the clumped distribution also indicates environmental conditions with spotty resource availability (Rahayu et al. 2010).

In general, banana plants grow vegetatively with suckers close to the parent. However, wild banana seeds can spread to more distant places via the dispersal agents by wild animals. At maturity, the fruits are eaten by wild animals such as primates, boars, birds, and bats. Seeds are germinable as soon as they have

Table 7 External factors analysis summary for conservation strategy of the wild bananas in Bromo Tengger Semeru National Park (BTSNP)

External factors	Weights	Rating	Score
Opportunities (O)			
There is an ex-situ conservation organisation in Pasuruan, East Java near BTSNP: PBG, in the form of living collections and seed banks	0.15	4	0.60
Research related to the conservation, diversity and bioprospection of wild bananas is currently becoming the world's spotlight to address global threats in modern bananas	0.15	4	0.60
Bioprospection studies of wild bananas for functional food, health, cosmetics, etc., are wide open with support from local academics/colleagues and the government (competitive)	0.13	4	0.52
Communities around BTSNP have the ability to cultivate bananas that support on-farm conservation. Wild bananas produce good quality of leaves which are prospected as natural fibers and can be used for animals feed	0.10	2	0.20
Subtotal O	0.53		1.92
Threats (T)			
Human pressure; because wild bananas are considered weeds, colonise and dominate disturbed sites, so they are often cleared	0.20	4	0.80
Harvesting of wild bananas by the community for animals feed (stems, leaves, male buds and fruits) and food packaging (leaves), etc. particularly at lower elevations (closer to settlement areas)	0.12	3	0.36
Encroachment of conservation forest to production forest by community	0.10	3	0.30
Wild animals consume wild bananas, including their fruits, male buds, shoots, young leaves, suckers, etc	0.05	1	0.05
Subtotal T	0.47		1.51
Total OT	1.00		3.43

been removed from the mature fruits. Nevertheless, in nature, seeds remain viable for months or even years; and as soon as favorable conditions become available, the seeds germinate vigorously (Nasution 1991). Then, the seedlings grow larger and form clumps vegetatively with suckers.

Wild banana *M. acuminata* communities were found more abundant at higher elevations > 1300 m asl than lower elevations. Juvenile and mature-vegetative plants dominated the population structure of wild banana *M. acuminata* in BTSNP, followed by suckers. Meanwhile, mature-generative plants are the smallest in proportion and mostly found at higher elevations (Fig. 4). Banana is a monocarpic plant. Individual plant may produce fruit all your round depending on its age. In the tropics, banana plant started to flowers in 7–9 months and completes its first fruit harvest in about 12 months regardless of the season (Chaurasia et al. 2017). As for wild seeded bananas require longer time for the fruits and seeds to ripen. Since the fieldwork was conducted in rainy season, a large number of suckers and juveniles emerged, about 26.20% and 36.37% of the population structure, respectively. However, the number of mature-vegetative individuals also considered high, reached 35.54% of the population that might enter the mature-generative (flowering and fruiting) soon.

The population structure based on plant stages is important to ensure sustainable population growth (Chu and Adler 2014). A normally distributed population structure suggests a healthy and sustainable structure. The abundance and structure of wild banana populations in BTSNP are thought to be related to differences in environmental conditions, which was confirmed by the PCA scatter biplot. The environmental characteristics pattern at lower elevations of ≤ 1000 m asl (Population 1) was clearly different from higher elevations of > 1000 m asl (Populations 2, 3, 4) (Fig. 5). The land slopes at higher elevations were found to be steeper. Since wild banana *M. acuminata* is not tolerant of poor drainage, resulting a tendency for them to be more abundant on slopes than plains (Nasution 1991; Vu et al. 2023). In the wild forest, *M. acuminata* is reported to be in stratum D (Ewusie 1980) since the height of the plant is < 10 m. It can be found in disturbed areas such as farm or plantation boundaries, rocky cliffs, deep ravines in the mountains, roads, and track edges (Marod et al. 2010).

Soil chemical content at higher elevations tended to have higher average values than at lower elevations. However, the soil pH at all populations was considered neutral, high organic C, moderate total N, low C/N, high to very high P Bray, low to moderate K, low to moderate Na, moderate Ca, low to moderate Mg, moderate CEC, and moderate BS. The soil texture in BTSNP was categorised as loamy, characterised as fertile, well drained, and easy to work (Table 3). At higher elevations, the soil composition was more sandy, thus more porous and loose (Bulmer and Simpson 2005).

The level of threats from human pressure is also thought to be the reason for the abundance of wild banana populations at higher elevations. At lower elevations close to settlements, habitat disturbance and harvesting of wild bananas for various purposes may occur. Whereas at higher elevations and steeper terrain, they tend to be safer and more conserved. Most local people consider wild banana as a weed that colonises and occupies open and disturbed areas, hence it is often cleared. Indeed, wild banana *M. acuminata* is acknowledged as "jungle weeds" that invades and dominates disturbed environments (Kallow et al. 2020). In addition, some local people harvest wild bananas in nearby forests for animals fodder (stems, leaves, male buds, and fruits) and food packaging (leaves), etc. (Hapsari et al. 2017). In particular, the extraction of male buds and fruits by humans and wild animals is also probably to be the main cause of the low number of mature-generative banana plants (flowering and fruiting) in population structure.

Based on the results of phenotypic characterisation (Figs. 6 and 7), it is suggested that the samples of the wild banana populations of *M. acuminata* in BTSNP were identified as a complex variety of *M. acuminata* var. *rutilifes*, *nakaii* and *zebrina*. Wild banana *M. acuminata* was considered to be a species complex, a complicated species in which one population can be closely similar to another, with overlapping characteristic in forms, shapes, color, and sizes. Continuous variation and phenotypic plasticity in response to environmental modification have made this species a difficult taxonomic group (Nasution 1991). Molecular analysis using various methods is proposed to confirm this species identification.

Furthermore, hybridisation between varieties in nature is possible and is likely to be the cause of the emergence of the species/variety complex of *M. acuminata*. The pollens of wild banana *M. acuminata* are viable, reaching 99.76% (Damaiyani and Hapsari 2018). The flowers of *M. acuminata* were pollinated during the night to the morning from 5 pm to 7 am. The flowers produced jelly-like nectar with 22–25% sugar concentration to attract pollinators such as bats, birds, and insects (Itino et al. 1991).

Musa acuminata var. *nakaii* and *zebrina* have a high character resemblance. Both have a red–purple color beneath the leaves and black-purple blotches on the upper leaves. However, *M. acuminata* var. *nakaii* has hairy fruits with convolute bracts, meanwhile var. *zebrina* has glabrous fruits and coracoid bracts. On the other hand, *M. acuminata* var. *rutilifes* is clearly distinguished by its yellowish-green color in the petiole, midrib, and leaf; the fruit is small with a bottle-necked tip. These three varieties are widely distributed in Java at elevation ranging from 50 to 1500 m asl (Nasution 1991; Hapsari 2014).

The clustering pattern of wild banana *M. acuminata* populations in BTSNP based on phenotypic characters was separated into three groups. Populations 1 and 2 were separated as sister groups (groups I and II), characterised by purple bract external face, cream yellow anther color, and yellowish-cream dominant color of male flower (Figs. 6a–g and 7). Whereas, populations 3 and 4 were clustered together in group III, characterised by red–purple color of the bract external face, reddish anther color, and reddish dominant color of the male flower (Fig. 6b–h and 7). Therefore, based on its phenotypic characteristics and referred to Nasution (1991), it is mostly *M. acuminata* var. *rutilifes* occupies at lower elevations, while var. *nakaii* and/or *zebrina* occupy higher elevations. Although, in general, all three varieties are likely to be found at all elevations.

Furthermore, in terms of proportions, although not very clear due to overlapping characteristics, *M. acuminata* var. *rutilifes* is slightly higher than *nakaii* and/or *zebrina* (Fig. 8). The main discriminator between the three *M. acuminata* varieties is known to be their generative characteristics, especially the color of the male bud, anthers and male flowers. Higher ultraviolet light radiation and lower temperatures at higher elevations (Schoen and Schultz 2019) may be a preference for *M. acuminata* var. *nakaii* and *zebrina* in BTSNP, resulting in a reddish color of the plants. Based on the fieldwork, these species were mostly found in open areas with light intensities up to 21,370 lx.

Phenotypic diversity analysis at the landscape scale of BTSNP showed high polymorphic phenotypic characters, heterozygosity, and Shannon index. In detail, Population 3 had the highest phenotypic diversity, followed by Population 4, Population 2, and Population 1, respectively (Fig. 9). Hence, the phenotypic diversity of wild banana at higher elevations was considered to be richer than at lower elevations. Furthermore, the analysis of phenotypic variance revealed a high level of phenotypic differentiation between populations (Table 5). It indicated that the phenotypic differentiation of wild banana *M. acuminata* in BTNP was significantly related to geographical barriers of elevations.

However, in the total phenotypic variance, only 15% was attributed between populations and the remaining 85% was explained by individual differences within the population. Self-pollination in wild bananas was rare due to different flowering times. Thus, the high level of variation within a geographically isolated population is presumably caused by cross-pollination between individuals, which is then maintained by clonal propagation through suckers. In addition, a long-distance seed dispersal event might result in the establishment of a healthy population that is genetically similar to the source population, but with no or limited gene flow after colonisation times (Mertens et al. 2021b). Further population genetic studies with various markers are needed to confirm this phenotypic population result.

National strategies for crop wild relatives (including wild bananas) conservation particularly in Indonesia and generally in Southeast Asia, have not been developed yet (Rahman et al. 2019). Conservation of wild banana *M. acuminata* is crucial to be initiated for further banana breeding to better cope with climate impacts. Based on the results of this study, S and O dominate the SWOT matrix (Tables 6 and 7). Therefore, the suitable conservation strategy of wild banana in BTSNP is assertive or proactive, including in-situ, ex-situ, and on-farm. In-situ conservation will permit their natural evolution and ex-situ conservation will ensure the availability of material for plant breeders and reintroduction programs. Whilst, on-farm conservation will improve the processes of evolution and adaptation of wild bananas and landraces to their agro-ecosystems (Rahman et al. 2019; Dilebo et al. 2023).

Furthermore, an assertive strategy is to leverage strength to maximise opportunities (S–O) (Scolozzi et al. 2014). Some detailed action plans (S–O) are proposed for the wild banana conservation strategy in BTSNP, including:

- Outreach to stakeholders (BTSNP management and the community) regarding habitat suitability, population structure, and phenotypic and genetic diversity of wild bananas in BTSNP. This outreach also highlighted the high potential and urgency of conserving wild bananas. This action plan supported the in-situ conservation strategy.
- Public awareness not to consider wild bananas as useless weeds and not clear up wild bananas (sustainable management).
- Public awareness of harvesting wild bananas from the forest within reasonable limits (sustainable management).
- Initiation of on-farm conservation through efforts to cultivate wild bananas by the community to harvest the stems, leaves, male buds, and fruits.
- Encouragement to conduct research and publication related to wild banana bioprospecting to promote its utilisation.
- Ex-situ conservation efforts of wild bananas in PBG (the nearest botanical gardens to BTSNP) in the form of living collections (vegetative materials) and seed banks (generative materials) for medium to long-term safety backup. If supporting facilities and infrastructure are available, cryopreservation can also be carried out as a long-term conservation strategy.

Conclusions

The study conducted on the wild banana populations in Bromo Tengger Semeru National Park (BTSNP) in East Java, revealed that the distribution of *M. acuminata* populations were clustered abundantly in open areas with high light intensity and humidity. Juveniles and mature-vegetative individuals dominated the population structure, and the communities were more prevalent at higher elevations. Environmental conditions, such as land slope and soil properties, played a significant role in shaping the ecology of wild banana populations. Three varieties of *M. acuminata* were identified through phenotypic characterisation: *M. acuminata* var. *rutilifes*, *nakaii*, and *zebrina*. Notably, phenotypic differentiation strongly correlates with elevations, acting as a geographical barrier. The SWOT analysis showed that an assertive or proactive approach is recommended for the conservation strategy of wild bananas. This approach entails engaging stakeholders, raising public awareness, conducting research and publications, as well as implementing in-situ, on-farm, and ex-situ conservation methods. The results of this study, with the BTSNP as a showcase, may become an initative pilot project in efforts to conserve important but neglected wild bananas, particularly in the wild forests of Indonesia and Southeast Asia in general, as a valuable genetic resource for the improvement of bananas in the future.

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Declarations

Conflict of interest The authors declare no competing interests.

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