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Ecological Characterization of Syzygium (Myrtaceae) in Papua New Guinea

Kipiro Qizac Damas[1], Silvio Cianciullo[2], Michele De Sanctis[2], Riccardo Testolin[2], Alessio Farcomeni[3], Abe Hitofumi[4], Vojtech Novotny[5], Paul Dargusch[6], Fabio Attorre[2]

[1]Papua New Guinea Forest Research Institute, Morobe Province, Papua New Guinea
[2]Sapienza University, Rome, Italy
[3]University of Rome Tor Vergata, Rome, Italy
[4]Papua New Guinea Food and Agriculture Organization, East Sepik Province, Papua New Guinea
[5]Biology Centre, Czech Academy of Sciences, Institute of Entomology and University of South Bohemia, South Bohemia, Czech Republic
[6]University of Queensland, Queensland, Australia

Email: kippyson@gmail.com

Abstract

Syzygium is the largest woody genus of flowering plants in the world and one of the most important components of the forest vegetation in Papua New Guinea (PNG). Although the systematics of the genus is improving, a comprehensive appraisal of the environmental features and gradients of its species is still lacking. Our work aims to fill this gap by analyzing the georeferenced specimens collected at the Lae National Herbarium of PNG. A data set of 1,563 records of 131 species was used to assess their altitudinal gradients and the correspondence with the main vegetation types and to model their spatial ecological niche with respect to climatic, topographical, and pedological variables. Several species were found to be widely distributed throughout the region, while other species were restricted to narrow altitudinal belts or only occurred in specific vegetation types. Overall, the genus is also characterized by an increasing altitudinal turnover likely due to topography-driven isolation. The improved knowledge of the ecological requirements of Syzygium assists in the elaboration of effective

conservation strategies and improves in situ species identification of this taxonomically difficult group.

Keywords

Topography-driven isolation, altitudinal gradients, Syzygium

Introduction

Syzygium R.Br. Ex Gaertn belongs to the Myrtaceae family and is the largest genus of woody flowering plants with about 1,200–1,800 species distributed throughout the Old-World tropics and subtropics [1, 2]. The greatest species diversity of Syzygium occurs in Southeastern Asia, Malesia, Northeastern Australia, and New Caledonia, while its greatest morphological and evolutionary diversity is within the Australian-Melanesian region [3, 4]. In Papua New Guinea (PNG), Syzygium is mainly represented by rainforest tree species widely distributed from the lowlands up to the highest elevations at about 4,000 m a.s.l. [5] presenting a broad variation of traits, even in response to abiotic factors, such as, for example, the degree of leaf venation in S. Buettnerianum along an altitudinal gradient [6]. Their flowers are important for a wide range of pollinators, while the fleshy and succulent fruits attract several mammals and birds. The first comprehensive review of Syzygium in PNG [6] recognized 138 species and more recent studies [7–11] have concluded that there are 207 species in the region, of which 84% are endemic [12]. However, the taxonomy of the genus remains a challenge, and uncertainties have been highlighted [13] and explored with in DNA studies [14]. Based on their results, Craven et al. [5] proposed the transfer to Syzygium of previously independent genera, such as Acmena, Acmenosperma, Cleistocalyx, Piliocalyx, and Waterhousea. Moreover, an infrageneric classification of the genus was presented as suggested by the inferred phylogeny [15]. In parallel with improvements in taxonomic knowledge, analyses on the spatial distribution and ecological preferences of Syzygium spp. In PNG are needed to support both forestry and conservation activities.

To achieve this aim, georeferenced Syzygium occurrences, held at the PNG National Herbarium of Lae (LAE), were analyzed with respect to pedological, climatic, altitudinal parameters and vegetation types.

Material and Methods

Data set

Lae hosts more than 2,000 specimens of Syzygium including information on latitude, longitude altitude, collection date, locality, and vegetation type. After checking for geographic and taxonomic inconsistencies, a final list of 131 species and 1,563 georeferenced records was obtained and used for analyses (table 1, figure 1). Environmental data include 19 bioclimatic variables, 3 soil variables, and slope. Climatic data were downloaded with a spatial resolution of 1 km from the Chelsa database [16], summarized in table 2. Soil data, such as organic carbon content, pH, and percentage of clay at 30 cm depth, were downloaded from SoilGrid [17] at 250 m spatial resolution. Slope was derived from a Digital Elevation Model with 90-m pixel resolution obtained from the NASA Shuttle Radar Topography Mission website.

Data analysis

To assess the completeness of the Syzygium data set, held by LAE, the estimates of species richness obtained by the asymptotic Chao 2 estimator [18, 19] were compared with randomized species accumulation curves.
To evaluate the variation of the composition of Syzygium sp. in PNG along the altitudinal gradient, two tests were conducted. The first one was designed to assess the similarity among adjacent 100 m altitudinal belts using the Jaccard index and the second considered all possible combination between all couples of altitudinal belts. Additionally, a detrended correspondence analysis was conducted to highlight the correspondence between altitudinal belts and Syzygium species. The correspondence between Syzygium species and vegetation types of the PNG forest map [20] was assessed using the indicator value index [21]. Vegetation types included coastal and swamp, lowland and montane forests, savanna and alpine grasslands, and heathlands.
A random forests (RF) model was used to model the spatial distribution of the Syzygium sp. with respect to climatic and soil variables. To this aim, only 40 Syzygium sp. with more than 10 occurrences were analyzed to reduce the uncertainties of the modeling procedure. To identify the most relevant variables in determining the distribution of Syzygium spp, the importance of the contribution of each variable accumulated along all nodes and all trees of the RF model were calculated [22].

Since the data set only contained presence data, in order to avoid overly optimistic predictions, pseudo-absences were estimated using random sampling without replacement, identifying a number of pseudo-absences equal to that of presences within known altitudinal ranges for the analyzed species. The quality for the fit of the model for each species was evaluated through the out-of-bag prediction error [23]. For each species, we repeatedly split the data in test and training sets. Each time, the model was built on the training set and used to predict the response on the test set, thus evaluating the prediction error. The average prediction error obtained was used for model evaluation. Probability distribution maps of the best model were then transformed into suitability maps by applying a threshold to each taxon to obtain a 0% omission error, which ensures that all the occurrences are correctly predicted. Data analysis was performed using the R statistical software [24] and geographical analysis was performed with QGIS software [25].

Results

The number of specimens collected during colonial times (before 1975) was higher compared with that collected afterward, even though a significant increase is expected in coming years due to the ongoing National Forest Inventory (figure 2). The difference between the sampling accumulation curve and the estimates produced by the Chao 2 estimator shows that a certain number of unknown species of Syzygium are yet to be collected and formally described (figure 3). Plotting the Syzygium samplings in the environmental space of PNG indicates that the genus mainly occupies warmer and drier areas characterized by annual precipitation below 3,000 mm and mean annual temperature above 20°C (figure 4). At higher elevations (using the altitudinal gradient), the similarity among altitudinal belts decreases significantly, in a linear way considering only adjacent belts (figure 5) and nonlinearly considering all possible distances (figure 6). Altitudinal belts and vegetation types are characterized by different Syzygium species, from the lowland distributed S. trivene and S. gonatanthum to the alpine S. alatum and S. benjaminum (figure 7, table 3). Moreover, Syzygium species, for which sufficient occurrences were available for modeling purposes, showed different suitability areas ranging from very narrow, such as the case of S. alatum, to widely spread, as S. amplum, which potentially covers more the 50% of PNG (figure 8, table 3). Such potential distributions are mainly determined by temperature variables, particularly the minimum temperature of coldest month (Bio6) and temperature seasonality (Bio4). Conversely, variables related to precipitation and soil parameters appeared to play a minor role (table 4).

Discussion

Syzygium is one of the most important tree genera of the PNG forest both in terms of biodiversity conservation, environmental integrity, and timber harvesting. Taxonomic knowledge has improved over time with 207 taxa currently recognized [12] and more species expected to be discovered [26]. However, knowledge about ecological features and environmental distribution is still incomplete. Despite the necessity to increase the field survey (figures 2 and 3), some preliminary patterns emerged. At the genus level, most specimens occupy drier and warmer areas of the country (figure 4). When looking at the altitudinal gradients, the nonlinear decrease of the similarity index among all belts seems to indicate the occurrence of widely distributed species, such as S. malaccense and S. stipulare (figure 6). However, the significant reduction of similarity among adjacent altitudinal belts seems to confirm the general pattern of increasing species turnover characterizing islands due to topography-driven isolation [27]. These patterns are determined by the differentiated spatial distribution of Syzygium species, confirming previous descriptions of vegetation types of PNG [28], with species widespread in lowland forest, S. trivene and S. stipulare, in the montane forest, S. subalatum and S. adelphicum, and in the alpine grasslands, S. alatum and S. benjaminum (figure 7, table 2). These species are characterized by different ecological niches and suitability areas as defined by the application of RF on a set of environmental variables (figure 8, table 3). The application of species distribution models on floristic data has already been applied in PNG, but previous attempts were based on aggregating data at the genus level significantly increasing the uncertainties of prediction [29]. Within a genus, species with very different environmental requirements can be found, as our study clearly indicates. Furthermore, this study confirms the usefulness of the analysis of herbarium data in support of biodiversity conservation strategies, also within the framework of the implementation of the REDD initiative in the county [30], and in facilitating the identification of species in the field for research investigation and forest management.

Conclusion

Knowledge of plant diversity in PNG is far from complete, with more detailed documentation of many species required and with many new species, to science, still to be identified and documented. This lack of knowledge has a significant negative impact on the elaboration of effective conservation strategies and on a more sustainable management of PNG forest ecosystems. The availability of herbarium data proved to be important for elucidating the habitat preference of Syzygium in PNG, when integrated with environmental data and modeling tools. Our case study focused on Syzygium, one of the richest genera in the country; through it, knowledge on the distribution and ecological features of its woody species has been significantly improved. The replicability of the proposed approach to other taxonomic groups, for which further studies are needed, is highlighted.

Case study questions

1. How important are herbarium data to improve the knowledge of plant species and to identify biodiversity hot spots?
2. How can herbarium data be used to guide new field surveys?
3. How can herbarium data be analyzed by means of species distribution models to improve the ecological knowledge of plant species?

Author contributions

Kipiro Qizac Damas defined the study, collected the herbarium data, and contributed to the discussion section. Silvio Cianciullo verified and evaluated the herbarium data, collected relevant environmental data, and conducted the modeling analysis. Riccardo Testolin and Alessio Farcomeni conducted the statistical analyses. Fabio Attorre prepared the preliminary draft of the manuscript. Michele De Sanctis, Abe Hitofumi, Vojtech Novotny, and Paul Dargusch reviewed, commented upon, and edited the manuscript.

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Competing interests

The authors have declared that no competing interests exist. Paul Dargusch is a section editor at CSE. He was not involved in the review process of this article. Fabio Attorre is a guest editor of the Papua New Guinea's Forests special collection. He was not involved in the review process of this article.

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Supporting information

Table S1 contains herbarium data in Excel format, which support the findings of this study.

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Tables

Table 1. Syzygium species and number of specimens collected at the Lae National Herbarium. Nomenclature follows Camara-Leret et al. [12].

Species	**n**	**Species**	**n**
Syzygium acuminatissimum	15	Syzygium nitidum	1
Syzygium acutangulum	24	Syzygium normanbiense	4
Syzygium adelphicum	41	Syzygium novoguineensis	1
Syzygium aeoranthum	3	Syzygium nutans	24
Syzygium alatum	34	Syzygium onesimum	3
Syzygium amplum	22	Syzygium pachycladum	20
Syzygium aqueum	49	Syzygium pallens	6
Syzygium attenuatum	4	Syzygium pergamaceum	10
Syzygium baeuerlenii	3	Syzygium phaeostictum	4
Syzygium benjaminum	30	Syzygium platypodum	7
Syzygium bicolor	4	Syzygium plumeum	10
Syzygium branderhorstii	21	Syzygium pluviatile	3
Syzygium brassii	1	Syzygium porphyrocarpum	15
Syzygium buettnerianum	38	Syzygium pseudomegistophyllum	1
Syzygium burepense	1	Syzygium pteropodum	8
Syzygium busuense	8	Syzygium puberulum	13
Syzygium callianthum	3	Syzygium pullenii	2
Syzygium capituliferum	1	Syzygium pyriforme	3
Syzygium carrii	1	Syzygium pyrocarpum	9
Syzygium cauliflorum	18	Syzygium racemoides	1
Syzygium cinctum	1	Syzygium recurvovenosum	2

Syzygium cladopterum	1	Syzygium richardsonianum	28
Syzygium claviflorum	11	Syzygium robbinsii	2
Syzygium coalitum	10	Syzygium roemeri	4
Syzygium cratermontensis	2	Syzygium rosaceum	6
Syzygium dansiei	1	Syzygium roseum	2
Syzygium decipiens	7	Syzygium rubropunctatum	1
Syzygium delicatulum	3	Syzygium sabangense	3
Syzygium dolichophyllum	8	Syzygium saliciforme	1
Syzygium effusum	87	Syzygium samarangense	29
Syzygium erythropetalum	12	Syzygium sambogense	2
Syzygium fastigiatum	7	Syzygium saundersii	3
Syzygium fibrosum	13	Syzygium sayeri	15
Syzygium flavescens	6	Syzygium schumannianum	4
Syzygium flavidum	1	Syzygium sessiliflorum	7
Syzygium forte	4	Syzygium sogerense	2
Syzygium furfuraceum	43	Syzygium sp	6
Syzygium gonatanthum	24	Syzygium stipulare	51
Syzygium goniocalyx	3	Syzygium subalatum	57
Syzygium goniopterum	6	Syzygium subamplexicaule	1
Syzygium grandifolium	2	Syzygium subcorymbosum	38
Syzygium hemilamprum	1	Syzygium subglobosum	1
Syzygium hemilamprum hemilamprium	3	Syzygium suborbiculare	3
Syzygium heterobotrys	1	Syzygium sylvicola	7
Syzygium homichlophilum	6	Syzygium synaptoneurum	2

Syzygium hylochare	8	Syzygium taeniatum	3
Syzygium hylophilum	53	Syzygium thalassicum	1
Syzygium insulare	5	Syzygium thornei	15
Syzygium iteophyllum	6	Syzygium tierneyanum	22
Syzygium kipidamasii	3	Syzygium trachyanthum	13
Syzygium lagerstroemioides	11	Syzygium triphlebium	2
Syzygium laqueatum	7	Syzygium trivene	73
Syzygium leonhardii	3	Syzygium tympananthum	1
Syzygium leptoneurum	3	Syzygium uniflorum	1
Syzygium leptophlebium	1	Syzygium validinerve	1
Syzygium leptopodium	26	Syzygium variabile	25
Syzygium longipes	37	Syzygium verniciflorum	4
Syzygium lorentzianum	10	Syzygium vernicosum	2
Syzygium macrocalyx	1	Syzygium versteegii	24
Syzygium madangense	1	Syzygium viburnoides	3
Syzygium malaccense	68	Syzygium waikaiunense	2
Syzygium megalospermum	8	Syzygium waterhousei	3
Syzygium megistophyllum	4	Syzygium womersleyii	36
Syzygium montana	11	Syzygium xylopiaceum	7
Syzygium naiadum	5	Syzygium zhenghei	38
Syzygium nemorale	10		

Table 2. Climate variables from CHELSA database used to model.

	Description		**Description**
Bio1	Annual mean temperature	Bio11	Mean temperature of coldest quarter
Bio2	Mean diurnal range	Bio12	Annual precipitation
Bio3	Isothermality	Bio13	Precipitation of wettest month
Bio4	Temperature seasonality	Bio14	Precipitation of driest month
Buio5	Maximum temperature of warmest month	Bio15	Precipitation seasonality
Bio6	Minimum temperature of coldest month	Bio16	Precipitation of wettest quarter
Bio7	Temperature annual range	Bio17	Precipitation of driest quarter
Bio8	Mean temperature of wettest quarter	Bio18	Precipitation of warmest quarter
Bio9	Mean temperature of driest quarter	Bio19	Precipitation of coldest quarter
Bio10	Mean temperature of warmest quarter		

Table 3. Syzygium species characterizing Papua New Guinea vegetation types based on indicator value analysis.

Species	**Coastal**	**Swamp**	**Lowland**	**Savanna**	**Montane**	**Alpine**
Syzygium capituliferum	x					
Syzygium hemilamprum	x					
Syzygium onesimum	x					
Syzygium roemeri	x					
Syzygium rubropunctatum	x					
Syzygium versteegii	x	x				
Syzygium amplum		x				
Syzygium branderhorstii		x	x			
Syzygium heterobotrys		x				
Syzygium leptophlebium		x				
Syzygium recurvovenosum		x				
Syzygium uniflorum		x				
Syzygium acutangulum			x			
Syzygium aqueum			x		x	
Syzygium buettnerianum			x			
Syzygium effusum			x		x	
Syzygium furfuraceum			x			
Syzygium gonatanthum			x			
Syzygium hylophilum			x			
Syzygium longipes			x			
Syzygium lorentzianum			x			
Syzygium malaccense			x			
Syzygium megalospermum			x			

Syzygium nemorale			x			
Syzygium nutans			x			
Syzygium pteropodum			x			
Syzygium richardsonianum			x		x	
Syzygium samarangense			x			
Syzygium stipulare			x			
Syzygium subcorymbosum			x			
Syzygium thornei			x			
Syzygium tierneyanum			x			
Syzygium trivene			x			
Syzygium brassii				x		
Syzygium coalitum				x		
Syzygium fibrosum				x		
Syzygium forte				x		
Syzygium puberulum				x		
Syzygium subamplexicaule				x		
Syzygium suborbiculare				x		
Syzygium adelphicum					x	x
Syzygium alatum					x	x
Syzygium benjaminum					x	x
Syzygium erythropetalum					x	
Syzygium laqueatum					x	
Syzygium leptopodium					x	
Syzygium montana					x	
Syzygium plumeum					x	

Syzygium porphyrocarpum					x	
Syzygium subalatum					x	
Syzygium sylvicola					x	
Syzygium variabile					x	
Syzygium womersleyii					x	
Syzygium zhenghei					x	

246 **Table 4.** Results of the Random Forests modeling on 40 Syzygium species with more than 10 occurrences.

Species	**N**	**Error %**	**Area%**	**Var1**	**Var2**	**Var3**
Syzygium acuminatissimum	15	54.8	50.0	bio4	Clay%	bio3
Syzygium acutangulum	24	22.3	30.9	bio2	bio7	bio6
Syzygium adelphicum	41	13.5	20.2	bio6	bio9	bio11
Syzygium alatum	34	8.4	8.9	bio6	bio9	bio5
Syzygium amplum	22	48.3	55.2	bio3	bio4	Slope
Syzygium aqueum	49	29.7	33.6	bio3	bio18	bio13
Syzygium benjaminum	30	13.4	13.4	bio6	bio8	bio11
Syzygium branderhorstii	21	18.8	33.6	bio11	bio6	bio1
Syzygium buettnerianum	38	33.5	40.2	bio13	bio16	bio4
Syzygium cauliflorum	18	29.7	34.1	bio13	bio16	bio17
Syzygium claviflorum	11	50.8	22.7	bio7	bio4	Org_C
Syzygium effusum	87	26.3	35.9	Slope	bio9	bio5
Syzygium erythropetalum	12	23.3	13.9	bio8	bio10	bio1
Syzygium fibrosum	13	18.8	16.2	bio15	bio14	bio10
Syzygium furfuraceum	43	32.4	36.3	bio15	bio4	bio3
Syzygium gonatanthum	24	30.8	14.6	bio8	bio18	bio4
Syzygium hylophilum	53	33.2	41.8	bio4	bio7	bio3
Syzygium lagerstroemioides	11	46.8	44.4	bio17	bio14	bio18
Syzygium leptopodium	26	21.8	15.9	bio13	bio6	bio16
Syzygium longipes	37	28.7	72.1	bio16	Org_C	bio13
Syzygium malaccense	68	32.3	53.0	bio4	bio3	Org_C
Syzygium montana	11	24.6	25.4	bio8	bio6	bio10
Syzygium nutans	24	33.5	63.2	bio13	bio15	bio16

Syzygium pachycladum	20	39.3	28.1	bio3	bio4	Org_C
Syzygium porphyrocarpum	15	23.7	28.7	bio14	bio17	bio12
Syzygium puberulum	13	25.1	12.2	bio17	bio19	bio14
Syzygium richardsonianum	28	36.0	44.6	bio3	Clay%	bio4
Syzygium samarangense	29	12.3	16.8	bio7	bio2	bio6
Syzygium sayeri	15	35.5	22.1	bio18	bio8	bio13
Syzygium stipulare	51	31.0	55.6	bio4	bio3	Org_C
Syzygium subalatum	57	25.3	44.7	bio6	bio1	bio10
Syzygium subcorymbosum	38	22.6	53.9	bio9	bio10	bio6
Syzygium thornei	15	37.6	14.0	bio4	bio3	CEC
Syzygium tierneyanum	22	31.6	50.4	Clay%	bio7	bio2
Syzygium trachyanthum	13	39.8	32.7	bio16	CEC	bio13
Syzygium trivene	73	14.1	23.1	bio4	bio3	bio15
Syzygium variabile	25	17.1	18.3	bio6	bio8	bio1
Syzygium versteegii	24	37.6	46.5	Slope	bio9	bio1
Syzygium womersleyii	36	20.9	24.5	bio6	bio9	bio11
Syzygium zhenghei	38	15.3	24.5	bio9	bio6	bio10

Note: N of occurrences, prediction error in percentage, potential suitable area in percentage and the first three important environmental variables are reported. CEC ¼ exchangeable cation; Org_C ¼ organic content.

Figures

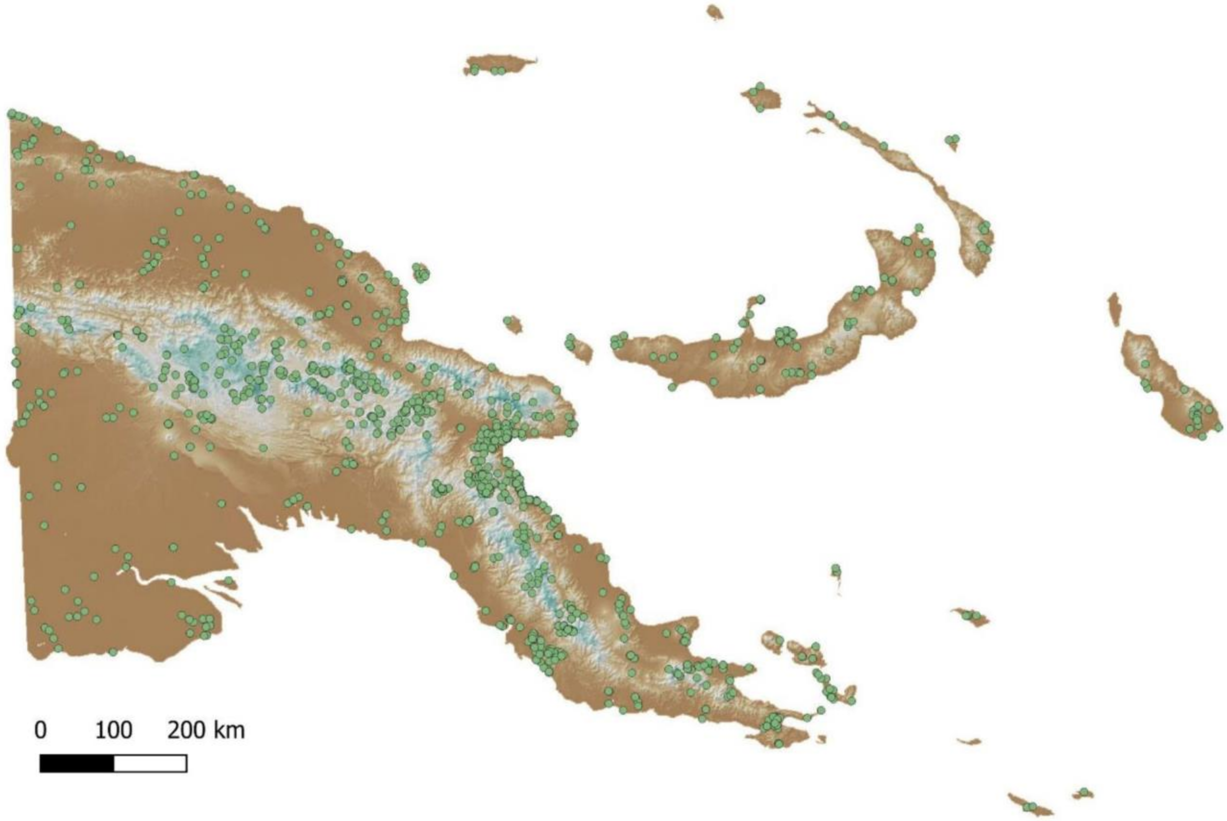

Figure 1. Distribution map of the collections of Syzygium species as held at the Papua New Guinea National Herbarium (Lae). Refer data in table S1.

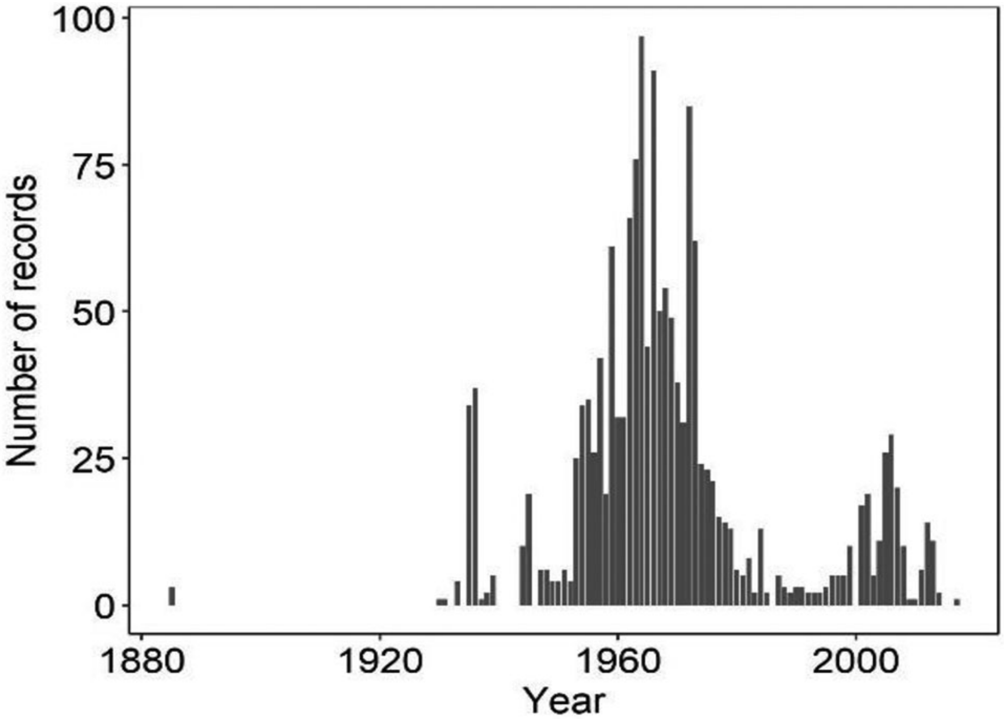

Figure 2. Syzygium specimens collected at Lae National erbarium (Papua New Guinea) during the last 140 years.

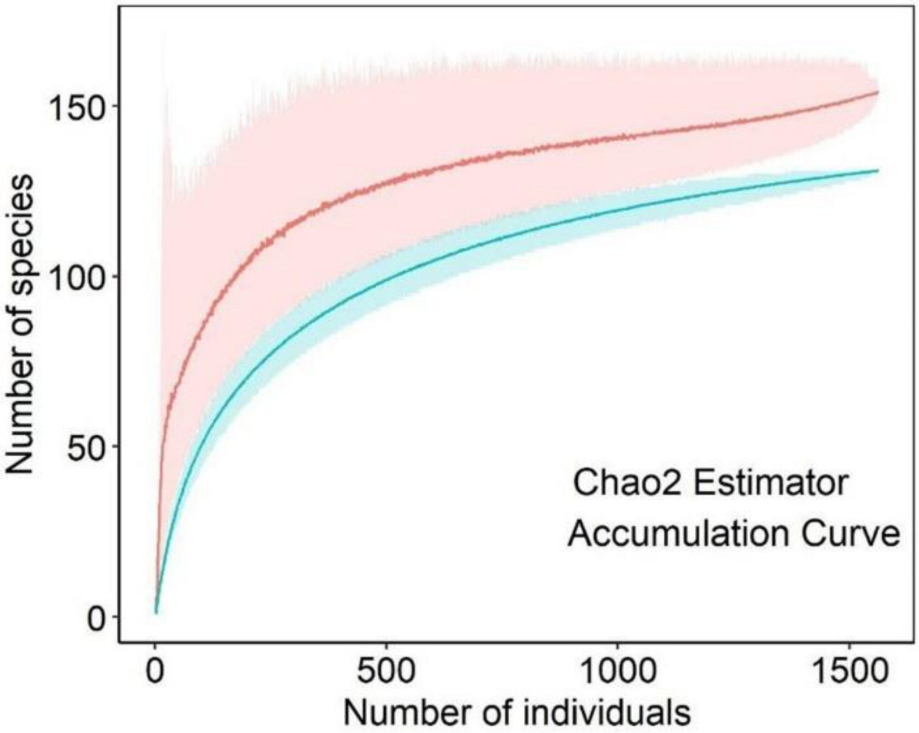

Figure 3. Accumulation curve (blue) and estimates using Chao 2 estimator (red).

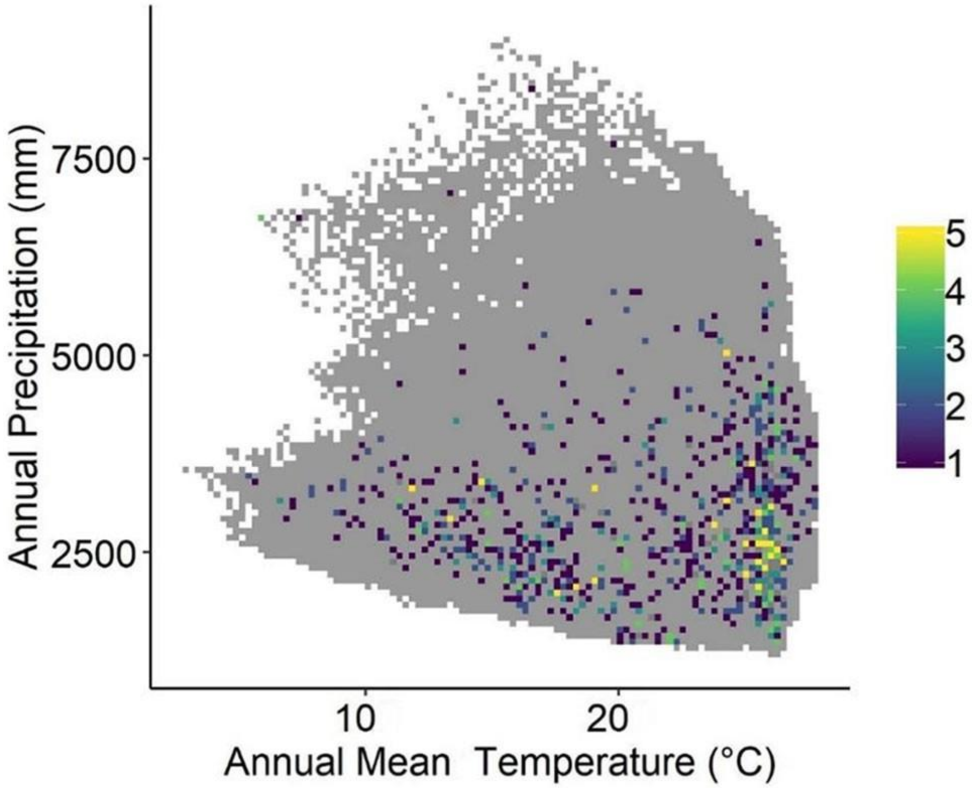

Figure 4. Scatterplot of Papua New Guinea environmental space as defined by annual precipitation and mean annual temperature (gray dots) and that occupied by Syzygium species grouped at genus level (purple to yellow according to the number of species per dot).

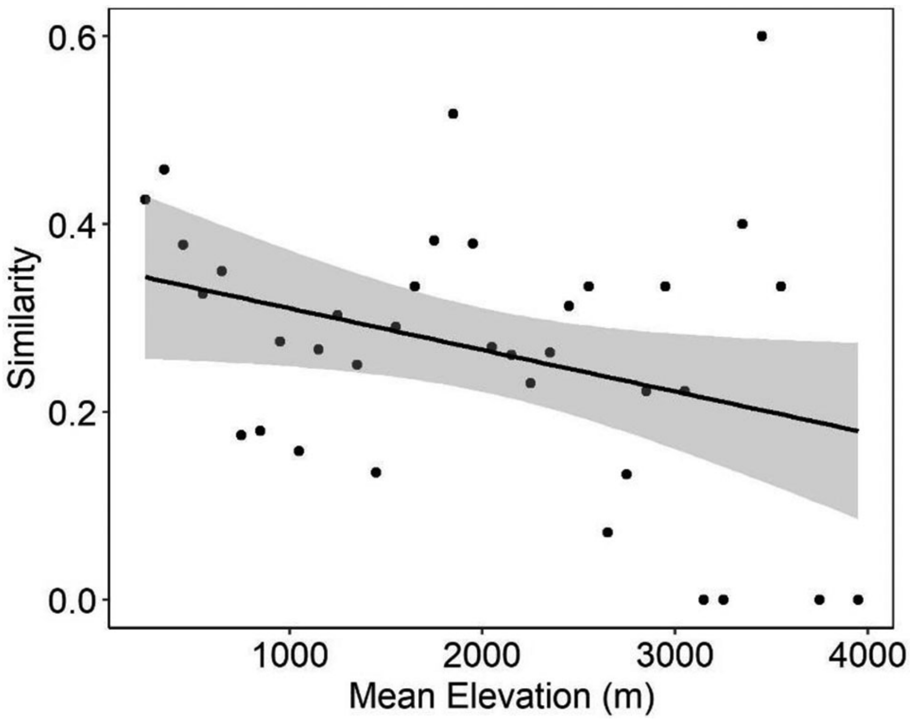

Figure 5. Similarity among adjacent 100 m altitudinal belts measured using the Jaccard method.

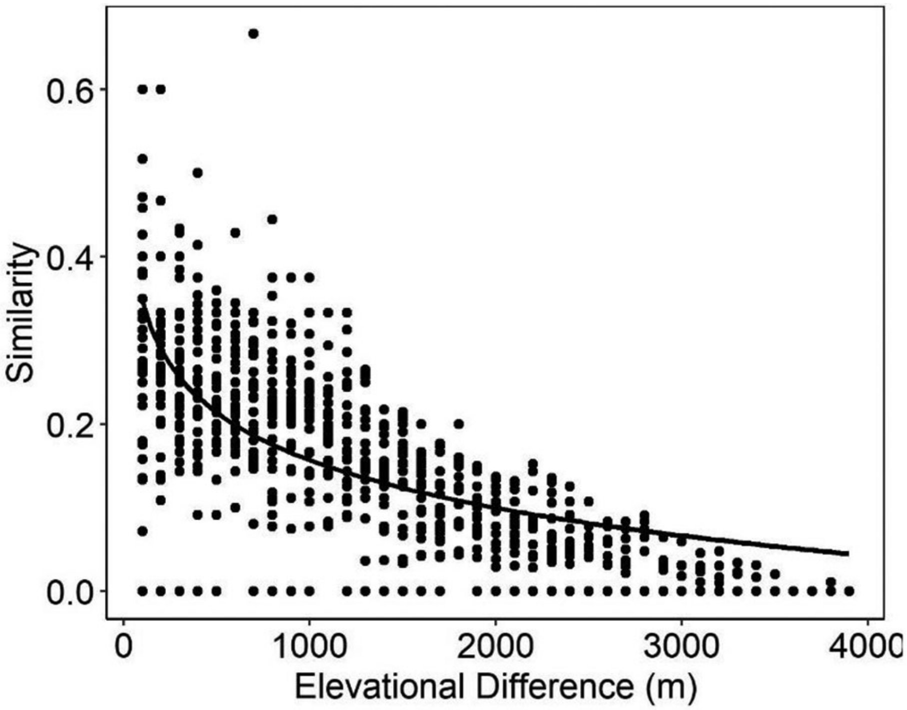

Figure 6. Similarity between all possible couples of 100 m altitudinal belts measured using the Jaccard method.

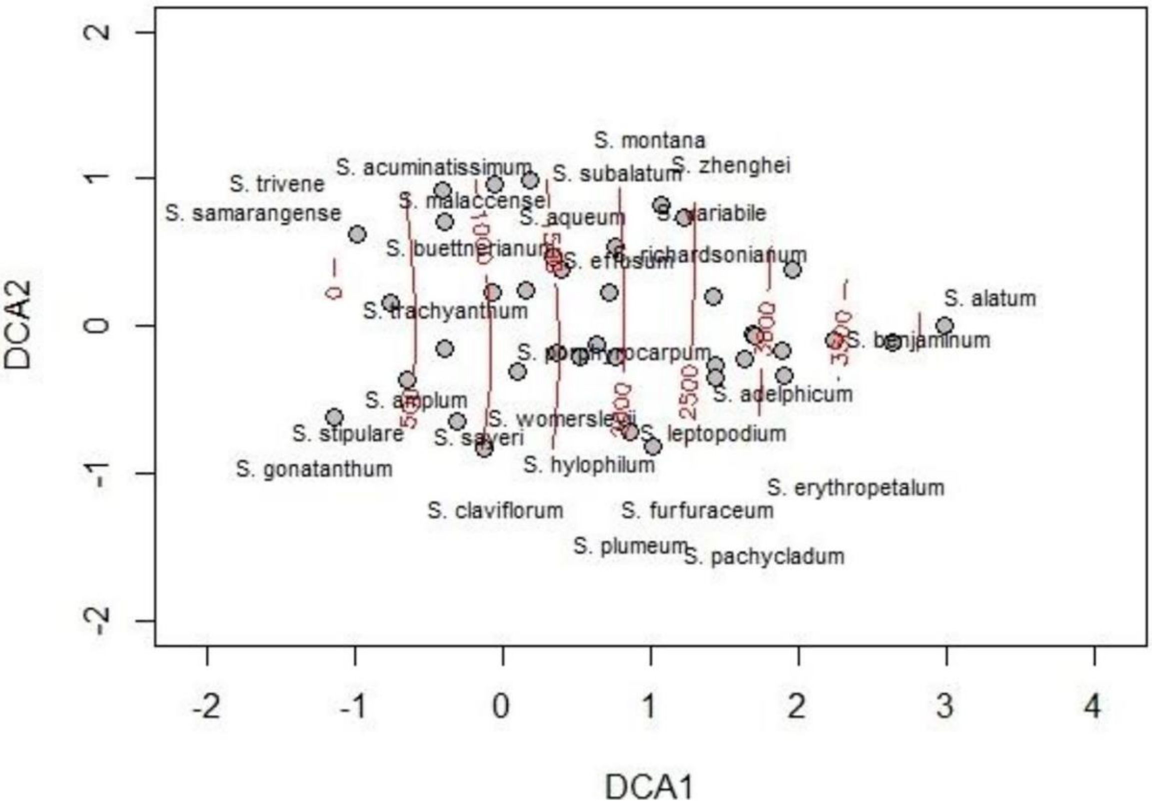

Figure 7. Detrended correspondence analysis of altitudinal belts and their Syzygium species composition.

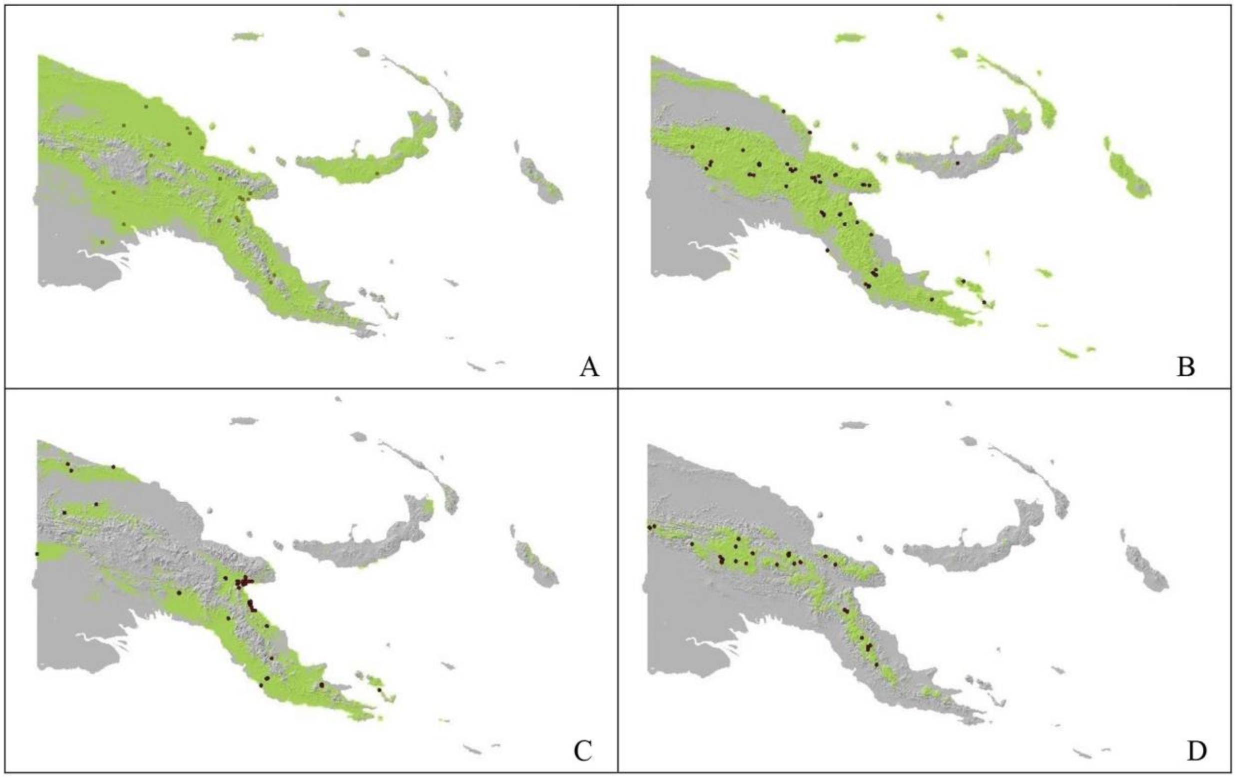

Figure 8. Example of suitability areas (in green) as predicted by random forests of (A) Syzygium amplum, (B) S. subalatum,(C) S. trivene, and (D) S. alatum. The black dots mark the occurrences for each species.