

Influence of spatial and environmental variables on rattan palm (Arecaceae) assemblage composition in Central Sulawesi, Indonesia

Joachim Thonhofer · Daniela Getto ·
Oliver van Straaten · Daniele Cicuzza ·
Michael Kessler

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Abstract Rattan palms are dominant elements of Southeast Asian rainforests and of high economic importance, yet little is known about the ecological factors determining the spatial distribution of species and assemblages. We studied rattan palm assemblages at two sites at different elevations in Lore Lindu National Park, Sulawesi, Indonesia (Pono: 958–1,266 m; Bariri: 1,390–1,507 m). At each site, we established a transect of 1.29 km consisting of 65 study plots of $10 \times 10 \text{ m}^2$ each, regularly spaced 20 m from each other. In total, we recorded 5,081 rattan individuals belonging to 22

species, with 1,367 individuals of 16 species at Pono and 3,714 individuals of 8 species at Bariri. Variance partitioning explained 29–49 % of community variation at Pono and 40–72 % at Bariri, with most variation jointly explained by spatial and environmental variables. Within the environmental influence, soil factors dominated over local topographical ones. RDA ordination allowed the discrimination of four species groups at Pono and three groups at Bariri. These groups were related to soil and less clearly to topographic variables. Our study is the first documentation of the importance of soil parameters in determining the spatial distribution of rattan palms. Interestingly, juvenile palms (<1 m tall) showed closer relationships to environmental factors than adult plants (>1 m tall), calling for further studies on the demography of rattan palms.

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J. Thonhofer
Institute of Botany and Landscape Ecology, Ernst-Moritz-Arndt-University Greifswald, Grimmer Str. 88,
17487 Greifswald, Germany
e-mail: joachim.thonhofer@gmx.de

D. Getto
Landscape Management and Nature Conservation,
University of Applied Science Eberswalde, Friedrich-Ebert-Str. 28, 16225 Eberswalde, Germany
e-mail: danielagetto@yahoo.de

O. van Straaten
Soil Science of Tropical and Subtropical Ecosystems,
Büsgen-Institute, University of Göttingen, Büsgenweg 2,
37077 Göttingen, Germany
e-mail: Oliver-van.Straaten@forst.uni-goettingen.de

D. Cicuzza
Center for Integrative Conservation, Xishuangbanna
Tropical Botanical Garden, Chinese Academy of
Sciences, Mengla, Mengla 666303, CN-Yunnan, China
e-mail: dcicuzza@gmail.com

M. Kessler (✉)
Institute of Systematic Botany, University of Zurich,
Zollikerstrasse 107, 8008 Zurich, Switzerland
e-mail: michael.kessler@systbot.uzh.ch

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Introduction

Understanding the spatial variation of tropical plant assemblages is of considerable theoretical and applied interest (Oliveira and Mori 1999; Slik et al. 2009). In particular, it is still unclear to what degree species distributions and the co-occurrence of the immense number of species are determined by environmental suitability and niche separation of species versus random but spatially autocorrelated seed dispersal (Condit et al. 2002; Tuomisto et al. 2003). While there is no question that both aspects play a role at certain spatial and temporal scales, there is also considerable variability between different plant and animal groups as well as possibly between geographical regions or habitats (Jones et al. 2013). Furthermore, both processes generate spatial structure in floristic data, so that simultaneous examination of spatial and environmental pattern in plant communities is needed to evaluate their relative importance (Borcard et al. 2004).

Palms are arguably the most emblematic tropical plant family. With over 2,600 species, they occur worldwide in tropical forests, with a few species also growing in arid habitats and reaching the southern limits of temperate regions. At the same time, palms are one of the economically most important plant families in tropical forests, being used as sources for food, oils, narcotic substances, and building materials, and are an important source of cash income, especially in rural areas. In both tropical lowland and montane forests, the spatial distribution of palm species has been shown to be related to soil and microtopographic conditions (Svenning 1999, 2001a; Eiserhardt et al. 2013), although there is also evidence of spatial population structure that may best be explained by dispersal processes (Svenning 2001b; Kristiansen et al. 2012). However, most of this research has taken place in the New World tropics where the majority of palms are free-standing. In contrast, much less is known about palms in the Old World tropics, where climbing rattan palms of the subfamily Calamoideae are often ecologically and economically the most important palm group (Gentry 1991).

Rattan palms are often abundant in Asian and Malaysian rainforest and have flexible stems that have for centuries been used for a wide variety of domestic, non-market purposes by rural communities (Dransfield and Manokaran 1993). Finally, they have become one of the World's most valuable non-timber forest products (Ros-Tonen 2000). Rattan palms comprise over 600 species (Uhl and Dransfield 1987) with the highest diversity of genera and species in western Malaysia (Dransfield and Manokaran 1993). On the Indonesian island Sulawesi, 56 rattan species have been recorded to date, with 37 in Lore Lindu National Park (LLNP) in Central Sulawesi, where they account for approximately 75 % of the palm flora (Dr. J.P. Mogeia, pers. com.).

Despite the high diversity and economic importance of rattan palms, surprisingly little is known about the ecological conditions determining the distribution and co-occurrence of rattan palm species (Siebert 1993, 2000, 2004; Bøgh 1996; Watanabe and Suzuki 2008; Stiegel et al. 2011). Rattan assemblage composition has showed to change with elevation (Siebert 2005), and reach maximum abundance and diversity at around 1,000 m (Appanah et al. 1993; Stiegel et al. 2011). Putz and Chai (1987) further found that local topography also plays a role, with seedlings and adult rattans being more abundant on ridges than in valleys. Regarding soil factors, specific studies are lacking, but it has been considered that soil drainage is crucial, so that most rattan species appear to prefer sites with good soil drainage (Watanabe and Suzuki 2008). Comparing trees and lianas, among angiosperms in general these different life forms are known to show somewhat different relationships to environmental conditions, with the distribution of lianas more closely linked to forest dynamics and hence less to abiotic site factors (Phillips et al. 2005; Macia et al. 2007; van der Heijden and Phillips 2008). Among palms, it is unknown whether climbing species also show this tendency.

In the present study, we explored the variation in rattan palm community composition at a local scale at two sites on the island of Sulawesi, Indonesia. Specifically, we aimed to determine the degree to which species distributions are related to environmental factors (soil and local topography) or show spatial structure that may be related to dispersal or other spatially structuring processes. Our assumption, based on the scant previous literature, was that abiotic

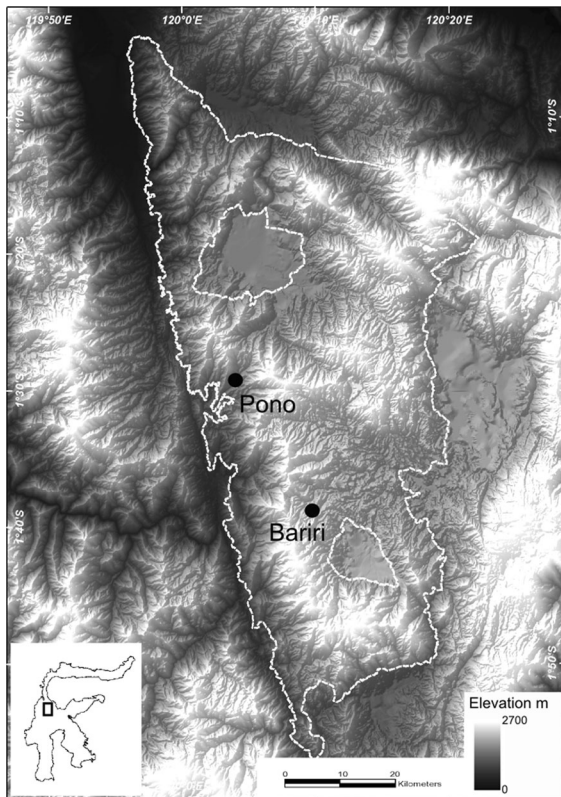


Fig. 1 Location of Lore Lindu National Park within Sulawesi (*inset*) and in central Sulawesi (park boundary marked by *white line*) as well as of the two study sites

factors (soils, local topography) show a lower relationship to rattan species distribution than spatial parameters.

Materials and methods

Study sites

Our study was carried out at two localities within the Lore Lindu National Park, Central Sulawesi, Indonesia (Fig. 1). The Pono site (S 01°29.6', E 120° 03.4', GC-WGS 84) was located in a sub-montane old growth forest at 958–1,266 m on Ferralsol (FAO 2006), developed on metamorphic rock (Culmsee and Pitopang 2009). The Bariri site (S 01°39.5', E 120°10.4', GC-WGS 84) was located about 22 km southeast of Pono at about 1,390–1,507 m elevation in lower montane old growth forest on Nitisol (FAO 2006), developed on sedimentary substrate (Culmsee and Pitopang 2009). Climatically, the study area has a

mean annual precipitation ranging from 1,900 to 2,100 mm (Hijmans et al. 2005; <http://www.worldclim.org/>), while mean annual temperatures range from 22.5 °C at 850 m to 19.0 °C at 1,500 m. Human impact was slight at both sites with no timber extraction, but showed differences especially with regard to rattan extraction. At Pono, rattan collection took place regularly for commercial purposes whereas at Bariri rattan harvesting was limited to local hunters collecting rattan occasionally for personal purposes as food or binding material (pers. obs.; local field assistants and local villagers, pers. com.).

Vegetation data

At both study sites, we established a transect of 1.29 km, to cover the local topographic variability of the forest. Each transect consisted of 65 non-permanent study plots of 10 × 10 m² each, regularly spaced 20 m from each other. These transects have previously been used to sample soil and vegetation data (Cicuzza et al. 2010; Willinghöfer et al. 2012; Jones et al. 2014).

In February and March 2008 we inventoried all rattan plants within the plots. Each plant that was spatially separated from others and was not obviously growing from a cluster was considered as an individual, although clonal rattan species can produce ramets several meters away from the mother plant (Uhl and Dransfield 1987). Each individual was classified as either adult (main stem > 1 m tall) or juvenile (stem < 1 m). Free-standing palms from subfamilies other than Calamoideae were not included in the study because of their different life form and because their low abundance (missing in > 2/3 of all plots) and diversity (3 species overall) in the study plots precluded quantitative analyses.

For field identification, we assigned each individual to morphologically distinguishable morphospecies based on standard traits used for rattan identification (Uhl and Dransfield 1987; Dransfield and Manokaran 1993, Dr. J.P. Mogege, pers. comm.). For convenience, these morphospecies were assigned field names mainly based on local names used by our field assistants. Because most rattan species on the island of Sulawesi remain undescribed (Dr. J.P. Mogege, pers. comm.), in the present study we treated these morphospecies as species and used the field names. All morphospecies were collected with three voucher

Table 1 Means and ranges (in parentheses) of the environmental variables in the 65 plots at each of the two study sites

Environmental parameter	Pono	Bariri
Elevation (m)***	1,067 (958–1,266)	1,434 (1,390–1,507)
Slope (°)	25.95 (0–45)	10.43 (0–45)
Aspect (°)	133.59 (0–340)	152.34 (0–350)
pH	3.91 (3.49–6.32)	3.92 (3.47–4.88)
C/N ratio*	12.71 (8.45–20.66)	11.53 (4.76–16.89)
C (%)***	3.51 (1.24–7.37)	2.40 (1.08–3.83)
N (%)***	0.28 (0.10–0.46)	0.22 (0.13–0.35)
Al (μmol/kg)***	31.31 (0.36–69.16)	17.88 (0.18–52.94)
Ca (μmol/kg)	27.64 (0.34–224.13)	19.79 (3.21–140.24)
Fe (μmol/kg)***	0.30 (0.03–1.44)	1.97 (0–11.02)
K (μmol/kg)***	3.41 (0.59–17.45)	1.17 (0.25–5.03)
Mg (μmol/kg)	9.16 (1.17–44.46)	14.15 (1.66–107.09)
Mn (μmol/kg)	0.58 (0.10–3.34)	3.90 (0.03–41.42)
Na (μmol/kg) ***	3.11 (0–6.25)	7.54 (0–26.19)
H (μmol/kg) **	1.45 (0–3.12)	1.00 (0–3.67)
CEC (cation exchange capacity) (μmol/kg)***	76.96 (34.23–249.78)	67.40 (22.25–257.67)
Bases (<i>S</i> Value) (μmol/kg)	43.32 (6.36–248.94)	42.65 (5.74–252.92)
Earth alkali saturation (<i>ES</i> Value) (μmol/kg)	27.75 (0.36–224.20)	19.94 (3.28–140.55)
Acidifier (<i>H</i> Value) (μmol/kg)***	33.33 (0.74–71.75)	22.78 (3.25–55.31)

Variables significantly differing based on *t* tests or Mann–Whitney *U* tests between the sites are marked with * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

specimens and deposited at the Herbarium Celebensis (CEL), the Herbarium Bogoriense (BO), and the Herbarium Göttingen (GOET).

Environmental and spatial data

Twenty-one environmental descriptors of each plot were either measured in the field or were derived from field measurements (Table 1).

Plot elevation (in m a.s.l.) was measured using a GPS (GPSMAP 96C, Garmin) at Pono. At Bariri relative elevation among plots was calculated from field measures of inclination taken from the center of each plot to the next plot on the same transect using a clinometer (Wilkie). Elevation values were initially calculated relative to the central plateau. These were then converted into absolute elevational values by adding GPS-measured elevation at the plateau to the relative elevation values. Slope inclination (in degrees) was measured using the clinometer incorporated in the compass. Plot aspect (in degrees) was measured with a compass and converted into two variables, northness [$\cos(\text{aspect})$] and eastness [$\sin(\text{aspect})$].

Mineral soil samples were taken at one point at the plot center from 0–10 cm depth for laboratory analysis at the University of Palu (Sulawesi). The values were

averaged out of two measurements. The soil chemical parameters analyzed were %C, %N, and their ratio, pH (in KCl), and Al, Ca, Fe, K, Mg, Mn and Na (all in μmol/kg). The latter six variables were *ln*-transformed prior to statistical analysis because plants are likely to respond more strongly on changes in nutrient availability at lower concentrations. pH is already logarithmic and aluminium was not transformed because it acts as plant poison at higher concentrations.

To identify spatial structure in the floristic data set, we created spatial variables within R (R Development Core Team 2010) Version 2.10.0, using the PCNM-method (principle coordinates of neighbour matrices) after Borcard and Legendre (2002). Following this procedure, the PCNM spatial coordinates were generated out of the *x*- and *y*-coordinates (UTM) of each plot center using the function quickPCNM (available at <http://biol09.biol.umontreal.ca/ULaval08/quickPCNM-77.R>). This function generates a large range of different spatial patterns at different scales, which allows us to include them into further analysis and test them for relevance.

Data analysis

To reduce the weight of the most abundant species within the floristic data set we Hellinger-transformed

Table 2 Species and numbers of individuals of rattan recorded in the 65 plots at each study site

Local name	Scientific name	Gf	Abundances		
			All	Juv.	Ad.
<i>Pono</i>					
Asli	<i>Calamus</i> sp. 1	S	376	311	66
Lambang	<i>Calamus ornatus</i> Blume var. <i>celebicus</i> Becc.	C	237	181	56
Noko	<i>Daemonorops macroptera</i> (Miq.) Becc.	S	226	216	10
<u>Humampu</u>	<u><i>Calamus</i> sp. 2</u>	C	223	143	80
Batang	<i>Calamus zollingeri</i> Becc.	C	139	120	19
Korthalsia	<i>Korthalsia celebica</i> Becc.	C	54	0	54
<u>Noko ibo</u>	<u><i>Daemonorops</i> sp. 1</u>	S	41	40	1
Paloe	<i>Calamus</i> sp. 3	C	37	24	13
Mpowaloo	<i>Calamus</i> sp. 4	S	21	17	4
Nona	<i>Calamus</i> sp. 5	N/A	7	2	5
Patani	<i>Calamus</i> sp. 6	N/A	5	4	1
Uban	<i>Calamus macrosphaerion</i> Becc.	N/A	5	4	1
Putih	<i>Calamus</i> sp. 7	N/A	2	0	2
Hulam	<i>Calamus</i> sp. 8	N/A	1	0	1
Kuru	<i>Calamus</i> sp. 9	N/A	1	0	1
Ombo	<i>Calamus</i> sp. 10	N/A	1	0	1
SUMS	16 species		1,367	1,052	315
<i>Bariri</i>					
Hilako	<i>Calamus</i> sp. 11	S	1,055	902	153
<u>Humampu</u>	<u><i>Calamus</i> sp. 2</u>	C	933	808	125
Pait	<i>Calamus</i> sp. 12	S	745	663	82
Uwe koi	<i>Calamus</i> sp. 13	C	357	303	54
<u>Noko ibo</u>	<u><i>Daemonorops</i> sp. 1</u>	S	324	322	2
Kuruku	<i>Calamus</i> sp. 14	S	178	136	42
Manda	<i>Calamus</i> sp. 15	S	119	98	21
Tohiti	<i>Calamus</i> sp. 16	N/A	3	1	2
SUMS	8 species		3,714	3,233	481

The two underlined species were shared between the two study sites. The growth form (Gf) indicates whether the species grow solitary (S) or clustering (C)

our species abundance data prior to analysis. This transformation makes species abundance data with many zeros usable for RDA (redundancy analysis) which is recommended for the purpose of variation partitioning (Legendre et al. 2005, 2009; Jones et al. 2008a). When comparing adults and juveniles, we rarefied the abundance of the more abundant category (usually juveniles) to that of the less abundant one, to avoid the bias of apparently stronger environmental correlations in groups with more individuals (Jones et al. 2008b).

For further analyses, the environmental variables were divided into two groups (“Soil” and “Topography”) to assess their respective contributions to variation in rattan species data. Principal component

analysis (PCA) was run to summarize variation in the Soil and Topographical variables into main axes, aiming to include at least 80 % of the variation of the parameters. To select the Soil, Topographic and Spatial variables that contributed significantly ($p < 0.05$ after 999 permutations) to the explanation of the variation in the rattan species composition, we ran multiple regressions with forward selection following the procedure of Blanchet et al. (2008) using “anova.cca” within the package “vegan” (Oksanen et al. 2008) and the function “forward.sel” within the package “packfor” of Stéphane Dray (available at http://r-forge.r-project.org/R/?group_id=195).

To quantify the different explanatory sources of the variation in rattan species composition, we used

Table 3 Factor loadings of the principal component analyses (PCA) of the environmental variables at the two study sites

Factors	Pono				Bariri				
	Soil1	Soil2	Soil3	Soil4	Soil1	Soil2	Soil3	Soil4	Soil5
C		−0.59	0.11	−0.37	0.14		−0.42	0.68	−0.11
N		−0.51	−0.26	−0.48		0.49	0.32	0.49	
C/N ratio		−0.24	0.65	0.13		−0.35	−0.62		−0.13
pH	0.29	−0.20		0.26	−0.26	−0.17	0.13	0.13	−0.33
Al	−0.31		−0.21		0.26	0.23	−0.29	−0.20	0.18
Ca	0.33		0.14	−0.14	−0.34	0.11			
Fe	−0.28	−0.15	−0.19		0.23	0.21	−0.10	−0.37	−0.19
K	0.23		−0.36			0.50			
Mg	0.28	0.16	−0.13	−0.12	−0.34	0.12			0.12
Mn	0.15	0.44		−0.48	−0.26	−0.13	−0.11	0.11	0.48
Na	−0.13		−0.32			0.32	−0.23		−0.56
H	−0.28	0.18	0.13	−0.36	0.31			−0.23	
CEC	0.26	−0.13	−0.33	0.29	−0.30	0.22	−0.27	−0.12	0.11
S value	0.34				−0.34	0.14	−0.13		
ES value	0.33		0.14	−0.14	−0.34	0.11			
H value	−0.33			−0.17	0.26	0.16	−0.22		0.46
Cum. proportion	0.53	0.68	0.77	0.84	0.49	0.62	0.73	0.79	0.85
Topography	Topo1	Topo2	Topo3		Topo1	Topo2	Topo3		
Elevation		−0.69	0.59			0.73	0.22		
Slope	−0.48	−0.38			0.41		−0.84		
Aspect	−0.63		0.18		0.64		0.24		
sine (aspect)	0.38	−0.57	−0.48		−0.59	0.16	−0.41		
cosine (aspect)	0.48	0.20	0.62		−0.26	−0.66	0.15		
Cum. proportion	0.44	0.71	0.87		0.41	0.68	0.85		

The cumulative proportion of variance captured by the axes (Cum. proportion) is also indicated

“variation partitioning” after Borcard et al. (1992). For this purpose we incorporated those Soil, Topographic and Spatial variables that were selected by the forward selection. The variation explained by the single selected variables was summed up within these analyses and assigned to the accordant group. The variation partitioning was carried out using the function “varpart” within the package “vegan”. The calculated R_{adj}^2 values were used to assess the proportions explained by the explanatory variable groups and their combinations. To test the significance of the variation explained, the different groups of variables were tested using the function “anova” within the package “vegan”.

To visually relate the occurrence of the individual species to environmental variables, we used RDA ordination. The RDA was carried out using the function “rda” within the package “vegan”. Only

species with abundances over 20 individuals per study site were included, these were 56 and 88 % of the species in Pono and Bariri, respectively. Finally, we used Spearman correlation analyses to identify species pairs whose abundances were significantly correlated.

Results

In total, we recorded 5,081 rattan individuals belonging to 22 species, with 1,367 individuals of 16 species at Pono and 3,714 individuals of 8 species at Bariri (Table 2). At Pono, each 100 m² plot contained from 0 to 57 rattan individuals (mean: 21; median: 20) and from 0 to 9 species (mean: 4; median: 4). At Bariri, numbers of rattan individuals per plot ranged from 12 to 291 (mean: 57; median: 48) and number of rattan

Table 4 R^2_{adj} values of the multiple regression analyses using the PCA axes recovered for the significant soil and topographic variables (see Table 2)

Factors	Pono				Bariri				
	Soil1	Soil2	Soil3	Soil4	Soil1	Soil2	Soil3	Soil4	Soil5
Full set	0.23	0.03	0.07		0.33		0.03		0.03
Juveniles	0.23		0.05	0.02	0.22		0.02		0.05
Adults	0.09	0.02	0.03	0.02	0.16		0.02		0.04
Topography	Topo1	Topo2	Topo3		Topo1	Topo2	Topo3		
	Full set	0.03	0.14	0.03			0.07	0.07	
Juveniles		0.12	0.02			0.03	0.06		
Adults	0.04	0.03					0.03		

Factors in bold show the highest values

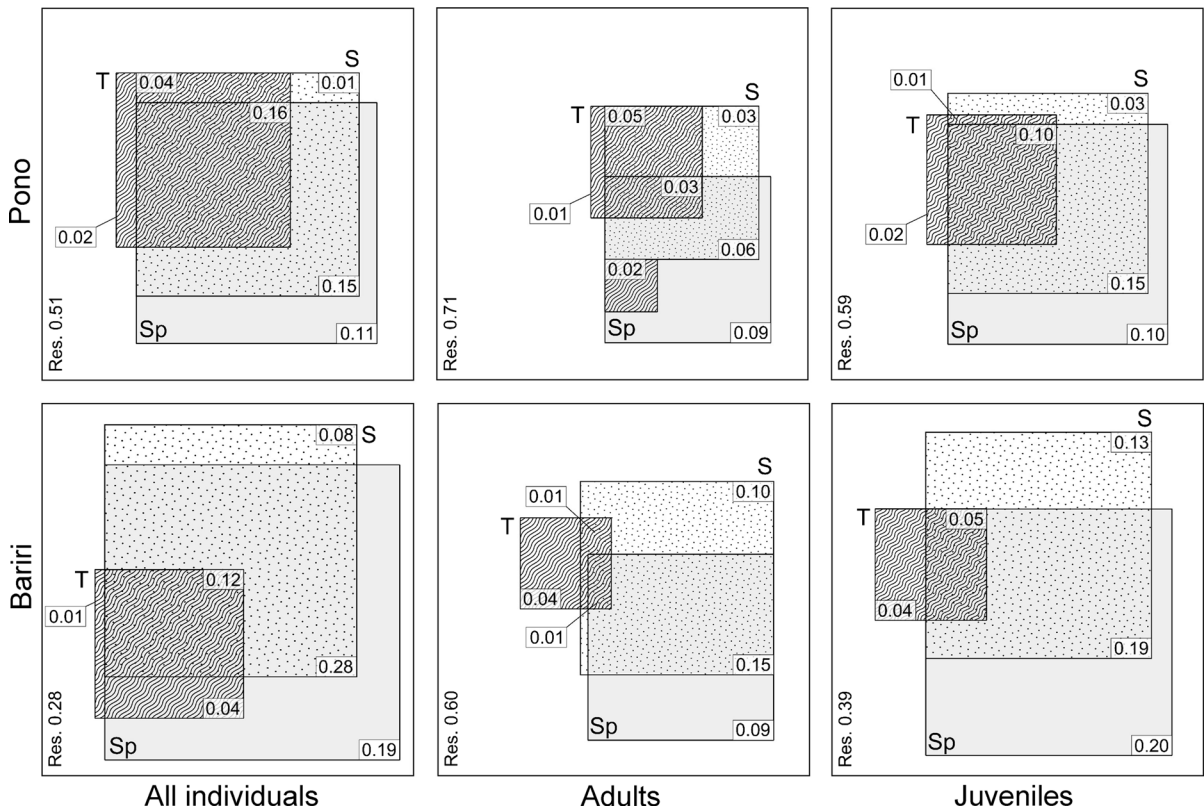


Fig. 2 Venn diagrams depicting the variation partitioning of the explanatory power of Soil (S), local Topography (T) and Space (Sp) for rattan assemblage composition at the two study sites, for all individuals combined, and for adults and juveniles

separately. The squares within the box approximately indicate the fraction of the explained variation of the single data sets. R^2_{adj} values of their exact contributions and their intersections are given within the Venn diagram

species from 2 to 7 (mean: 5; median: 5). Of the 22 morphospecies, 5 could be assigned to an already described species, all others are probably undescribed (Dr. J.P. Mogege, pers. comm.).

The proportion of juvenile plants recorded per species (76.4–99.4 %) was significantly higher than that of adults (0.6–23.6 %) (*G* test, $p < 0.001$), except for *Korthalsia celebica* at Pono, of which only adults

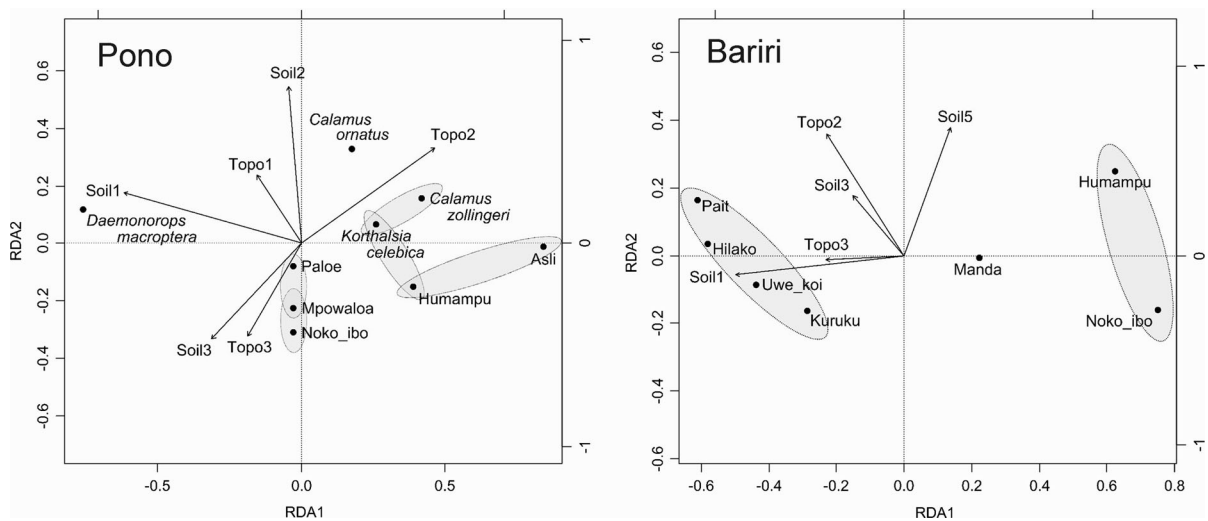


Fig. 3 RDA ordinations for Pono and Bariri based on the full species data set (all individuals). Gray ovals enclose species whose abundances were significantly positively correlated

were found (Table 2). The proportion of juveniles and adults per species did not differ between sites (t test, $p > 0.1$). When separated by growth form (solitary versus clustering), we found that at Pono there were fewer solitary species than at Bariri (44 vs 71 %) (G test, not significant) as well as individuals (49 vs 65 %) (G test, $p < 0.01$), which was mainly due to a paucity of adult plants of solitary species (27 vs 63 %) (G test, $p < 0.001$).

The PCA combined the 21 environmental variables into four Soil and three Topographic PCA axes for Pono and five Soil and three Topographic axes at Bariri (Table 3). At both sites, PCA axes Soil1 were correlated to pH values and cation loads, whereas axes Soil2 were correlated to N concentrations (and to C concentrations at Pono). Axes Topo1 included mainly information about slope and aspect, whereas Topo2 was mainly correlated to elevation. Multiple regression analyses selected 4–6 variables with the most important being Soil1 at both sites whereas for Topography at Pono Topo2 and at Bariri Topo2 and Topo3 (which included information about slope inclination) were selected (Table 4). At both sites, R^2_{adj} values of juveniles exceeded those of adults.

Variance partitioning showed that all three variable groups (Soil, Topography and Space) contributed significantly ($p < 0.001$ after 999 permutations) to rattan species composition at both study sites and for all data sets (all plants, juveniles, adults) (Fig. 2). Explained variation ranged from 29 to 49 % at Pono

and from 40 to 72 % at Bariri. Space and Environment both had a small individual contribution to variance explained (6–20 %) whereas the variation jointly explained by Space and Environment was larger (11–44 %). Explanatory power was conspicuously higher for juvenile plants than for adults, even after accounting for differences in numbers of individuals (Fig. 2). Splitting the component of environmental influence into Soil and Topography showed that the explanatory power of Soil exceeded that of Topography for all data sets. Additionally, the amount of redundant variation (explained by more than one variable group) was high for all data sets and exceeded the explanatory power that could be assigned purely to the single variable groups. Especially Soil and Space showed marked overlaps (Fig. 2).

RDA ordination showed that at Pono, four species groups could be identified (Fig. 3). *Daemonorops macroptera* and *Calamus ornatus* var. *celebicus* were placed far apart from the other species in the ordination and indeed, the abundance of *Daemonorops macroptera* was significantly negatively correlated to that of most other species. The remaining species were placed in two groups, one formed by Mpowaloe, Noko ibo and Paloe, and the other by Asli, *Calamus zollingeri*, Humampu and *Korthalsia celebica*. At Bariri, Humampu and Noko ibo (the only two species shared with Pono) formed a group, four other species (Hilako, Kuruku, Pait, Uwe koi) formed another group and Manda was placed between the

two groups. At both sites, RDA axes 1 were associated with PCA axes Soil1 and less clearly with Topography (Topo2 at Pono, Topo3 at Bariri). Roughly the same patterns were retrieved when the analyses were conducted separately for juveniles and adults, although for adults the patterns and groups were less well defined (Fig. S1).

Discussion

Although our two study sites were only 22 km apart, they contained very different rattan assemblages that only shared two species. Partly, this difference reflects the elevational difference between the sites, with Pono located at 958–1,266 m and Bariri at 1,390–1,507 m. Previous studies have shown that rattan diversity peaks at about 1,000 m elevation and declines towards higher elevations both in the study region (Stiegel et al. 2011) and in Malaysia (Appanah et al. 1993). Terrestrial herbs are also more diverse at Pono (184 species) than at Bariri (135 species) (Cicuzza et al. 2010; Willinghöfer et al. 2012) whereas for trees, Pono is less diverse (74 species on 2,400 m²) than Bariri (123 species) (Culmsee and Pitopang 2009). Our results thus contrast with those of Watanabe and Suzuki (2008) who found a positive correlation of tree and rattan diversity in Borneo and Java, but their study covered lowland habitats whereas our research area was located at higher elevations where rattan diversity is already strongly in decline and may thus be independent of tree diversity.

The elevational difference between the study sites was thus not only related to changes in species numbers but also in assemblage composition. In Central Sulawesi, rattan assemblage composition changes strongly with elevation, with a complete turnover of species composition within 900 m elevational change (Stiegel et al. 2011). Furthermore, although Pono had twice the number of species, it only had roughly one-third the number of individuals compared to Bariri, so that species were on average about six times more abundant at the latter site.

Despite these floristic and ecological differences, the ecological factors related to the spatial distribution of the individual rattan species were surprisingly similar at both sites. With the available Soil, local Topographic and Spatial variables, it was possible to statistically explain between 29 and 72 % of variation

in rattan species composition. This range is comparable to that of previously performed studies on rainforest trees, which typically explain between one and three quarters of the floristic variation (e.g., Jones et al. 2008a; Slik et al. 2009). The unexplained variation (28–71 % in our case) can be attributed to stochastic variability in species distributions as well as unmeasured environmental factors (Jones et al. 2008b). In our study, much of the explained variation was shared between the groups of explanatory variables, in particular Soil and Space, so that a direct causal interpretation (which is problematic in any case for correlative studies such as this) must be made with care.

Nevertheless, we found that Soil-related factors tended to have stronger explanatory power than local Topography. The purely spatial component was also high in some of the analyses. This could reflect either the influence of unmeasured ecological factors that are spatially structured or the influence of dispersal processes and the corresponding patchy occurrence of rattan species in the landscape. The latter may be especially relevant in rattan species, as many of them are dioecious and reproduce clonally (Dransfield 1979; Dransfield and Manokaran 1993). Our data do not allow a direct evaluation of these alternatives. However, the RDA ordination suggests that rattan species in the study region are arranged in ecological guilds that use ecological niche space in different ways. This is most evident at Bariri, where the two rattan species shared with Pono grew at sites with a negative relationship to the PCA Soil1 axis, i.e., on soils of high pH and cation concentrations but low aluminium concentrations. Interestingly, these soil conditions approach those at Pono in some respects, and suggest that part of the spatial structure observed in the rattan assemblages is determined by ecological niche structuring involving soil parameters. On the other hand, the two rattan species shared by the two study sites group in the RDA ordination at Bariri, but not Pono. Closer examination of the data shows that the distributions of these species are linked to Soil parameters (Soil axis 1) which have much higher variability at Pono than at Bariri. Accordingly, it is possible that niche differentiations between these two species are only evident at Pono, where there is enough niche space to allow for niche differentiation. Naturally, other ecological parameters such as vegetation structure, light availability and host tree identity

are likely to also influence the distribution of rattan species (Siebert 1993).

Our study does not allow a quantitative comparison of the importance of environmental factors in structuring rattan assemblages relative to free-standing palms (of which there were too few in the study region for quantitative analyses) or trees (that were not sampled by us). We can nevertheless conclude that rattan palms in our study area show distinct spatial distribution patterns at the local scale, with groups of species forming ecologically distinct guilds especially with relation to soil parameters. Thus, this is the first study to document the importance of soil factors for the spatial niche separation of rattan species at a local scale. Soil factors are well known to be among the most important ecological parameters determining the spatial distribution of tree species in tropical forests, especially at small spatial scales such as those of our study (Condit et al. 2002; Tuomisto et al. 2003; Jones et al. 2011). Climbers are often considered to be less closely linked to soil factors than trees (Phillips et al. 2005; Macia et al. 2007; van der Heijden and Phillips 2008), but the results of our study does support this for rattan palms. Our study supports the general perception that soil conditions are crucial in determining the spatial variation of tropical plant assemblages (Oliveira and Mori 1999; Slik et al. 2009).

Perhaps the most interesting finding of our study is that juvenile rattan plants showed stronger statistical relationships to ecological factors and space than adult plants. Typically, ecological filtering is more likely to operate in the opposite way, namely that plants are more likely to survive at suitable sites and hence that adults show closer environmental relationships (Jones et al. 2008b). One possible explanation might be that germination and establishment of rattan palms is favoured in certain microhabitats, e.g., in relation to soil, but that adult survival is favoured under a different set of environmental conditions, perhaps determined by canopy structure and light availability (Siebert 1993). Alternatively, ecological site conditions may influence the reproductive output of mature plants, leading to patchily distributed cohorts of juveniles. These hypotheses require demographic and experimental evaluation, and may contribute to a more general understanding of how differing life history traits of juvenile and adult plants may lead to complex selective interactions with environmental factors.

Finally, some comments on the impact of rattan extraction on community composition may be appropriate. We found that in Pono, where there is some rattan extraction, there was a paucity of adult individuals of the solitary rattan species, i.e., those where extraction not only kills the adult plant but potentially also inhibits reproduction. While the rarity of mature plants is not surprising, it is interesting to note that this was not reflected in the relative abundances of young plants. We suspect that the high intensity of rattan extraction is fairly recent and that negative effects on recruitment will only become apparent in a few decades. Indeed, our field observations suggest that there may already be a low density of very young seedlings, although we do not have quantitative data to support this (J. Thonhofer & D. Getto, pers. obs.).

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