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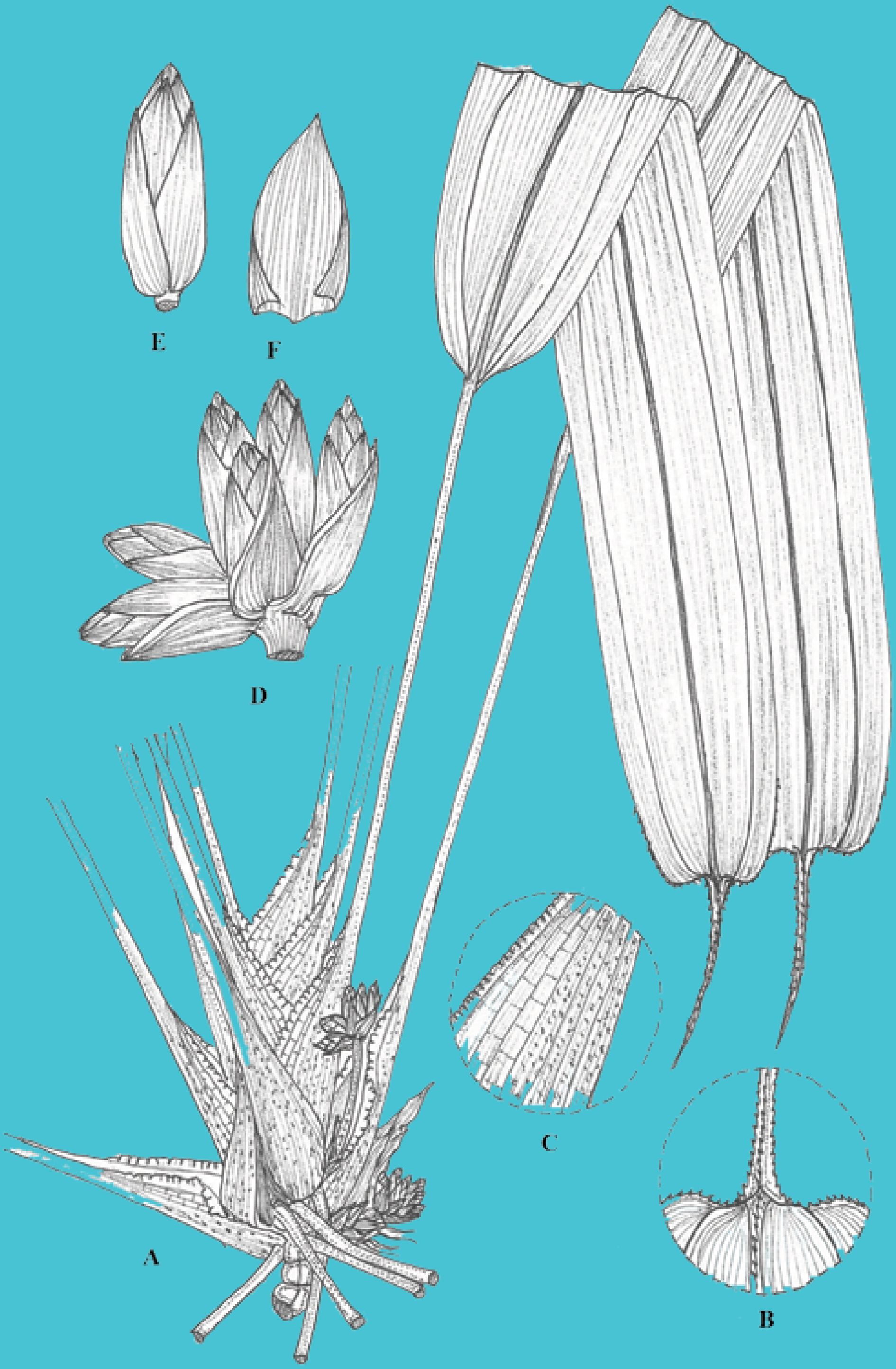

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# RATTAN DIVERSITY AND BROAD EDAPHIC NICHES IN A TROPICAL RAINFOREST OF BUTON, SULAWESI, INDONESIA

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## ABSTRACT

PRITCHETT, R., PHILLIPS, A., MARDIASTUTI, A. & POWLING, A. 2016. Rattan diversity and broad edaphic niches in a tropical rainforest of Buton, Sulawesi, Indonesia. *Reinwardtia* 15(2): 99 – 110. — This paper attempts to answer the question: how can at least 20 species of rattan palms in the genus *Calamus* (family Palmae (Arecaceae)) co-exist in a rainforest? A survey of rattans was made in Lambusango Forest on Buton, an island close to south east Sulawesi, in Indonesia. Rattan species and numbers were recorded in 87 quadrats of 30 × 10 m, laid out along linear transects in habitats with a variety of soils. Evidence for edaphic (soil) niches was sought. Different rattan species were found to be adapted to soils with different conductivity and pH values. Standardised mean difference (d) scores were calculated for pairs of species based on their response to soil pH. Of the 66 pairs tested, 61 were found to be significantly different statistically. Such differences suggest, but do not prove, that many species occupy different edaphic niches. It was found that species which show a preference for soils with intermediate pH values (5.0 to 6.5) can grow in soils with a wide range of pH values, implying broad edaphic niches and that competition between these species is weak. Correspondence analysis shows that many species do not distinguish greatly between many soils with intermediate pH values. It is concluded that rattan species show evidence for having different edaphic niches, although the niches for many species are broad. It is speculated that many rattan species may be ecologically equivalent and that a weak version of ecological neutrality theory may apply.

**Key words**: Neutrality, niches, rattan, soil, Sulawesi.

## ABSTRAK

PRITCHETT, R., PHILLIPS, A., MARDIASTUTI, A. & POWLING, A. 2016. Keanekaragaman rotan dan relung edafis yang luas di hutan hujan tropis Buton, Sulawesi, Indonesia. *Reinwardtia* 15(2) 99 – 110. — Tulisan ini mencoba untuk menjawab pertanyaan: bagaimana setidaknya 20 jenis rotan marga *Calamus* (suku Palmae (Arecaceae)) hidup berdampingan di hutan hujan? Sebuah survei rotan telah dilakukan di hutan Lambusango di Buton, sebuah pulau yang dekat dengan Sulawesi Tenggara, Indonesia. Jumlah jenis individu rotan yang direkam dari 87 petak 30 × 10 m, diletakkan di sepanjang garis transek pada habitat dari berbagai jenis tanah. Pengaruh terhadap relung edafis (tanah) dicari. Jenis rotan yang berbeda diduga ditemukan sesuai dengan tanah dengan konduktivitas dan pH yang berbeda nilainya. Nilai rata-rata perbedaan standarisasi (d) dihitung untuk jenis-jenis yang berpasangan berdasarkan respon mereka terhadap pH tanah. Dari 66 pasang diuji, 61 ditemukan secara signifikan berbeda secara statistik. Perbedaan tersebut menyarankan, tapi tidak membuktikan, bahwa banyak jenis menempati relung edafis berbeda. Ditemukan bahwa jenis yang menunjukkan preferensi untuk tanah dengan pH menengah (5.0-6.5) dapat tumbuh di tanah dengan berbagai nilai pH, menyiratkan relung edafis yang luas dan bahwa persaingan antar jenis ini lemah. Analisis korespondensi menunjukkan bahwa banyak jenis rotan tidak terlalu berbeda diantara jenis tanah dengan nilai pH menengah Disimpulkan bahwa jenis rotan menunjukkan bahwa mereka memiliki relung edafis yang berbeda, meskipun banyak jenis memiliki relung yang luas. Hal ini menimbulkan spekulasi bahwa banyak jenis rotan mungkin secara ekologi setara dan bahwa teori netralitas ekologi mungkin berlaku walaupun masih belum terlalu kuat.

**Kata kunci**: Netralitas, relung, rotan, Sulawesi, tanah.

## INTRODUCTION

A central question of ecology is how can so many species of the same trophic level co-exist in a habitat without one species out-competing the others and causing their local extinction? This problem is of particular relevance to plants, where different species compete for a very limited range of environmental resources, namely light, water and a few mineral nutrients (Silvertown, 2004). One explanation is that each species is adapted to an ecological niche: a set of environmental and biotic resources which allows it to persist; even in the presence of other species, each of which is adapted to a different set of resources (Hutchinson, 1978; Colwell & Rangel, 2009). Such adaptation involves 'trade-offs' (Grime, 2001).

If species do exploit niches there should be distinct differences between species and a consequence would be that individuals within species should increase in number when rare, since the resources on which they depend would be under-exploited (Levine & HilleRisLambers, 2009; Wilson, 2011). This frequency dependence would be due to intraspecific competition being greater than interspecific competition.

An alternative explanation for the co-existence of species has been offered by Hubbell (2001). This explanation assumes that all individuals of all species present are ecologically equivalent; hence species are 'neutral', in that no species is assumed to be competitively superior to others. Such a theory is offered as useful in ecological research for its descriptive and predictive powers, even though it is understood that the world is not strictly neutral. Rather it assumes that differences are not functionally significant (Hubbell, 2001; Rosindell *et al.*, 2012; Matthews & Whittaker, 2014). The theory of neutrality suggests that replacement of one species by another can be a very slow process, occurring on the same time scale as speciation (Hubbell, 2001).

The problem of co-existence of similar and possibly competing species applies to the rattans, which are climbing palms (family Palmae (Arecaceae), sub-family Calamoideae) requiring forest trees for support (Dransfield *et al.*, 2008). Since many are congeneric and have the same general way of life they might be expected to compete ecologically with each other.

At least 20 species of rattans, all classified in the genus *Calamus*, have been found in Lambusango Forest on the island of Buton, situated close to (10 km at nearest) the coast of south east Sulawesi, in Indonesia (Widayati & Carlisle, 2012; Powling *et al.*, 2015). The forest, part of which is a wildlife reserve, has a wide variety of habitats. In altitude it runs from 0 to 700 m, with rainfall over 2000 mm per year, and a variety of underlying rocks (Milsom, 2000; Powling *et al.*, 2015). The rocks include limestones, sandstones, chert and peridotite, the last of these giving rise to ultrabasic (ultramafic) soils. Thus the forest has very diverse topography and soils, and many different forest types exist (Powling *et al.*, 2015). The heteroge-neity of the habitats suggests that much 'niche space' is available to plants, so many different ecological niches should be available for different species to occupy (Colwell & Rangel, 2009). This could account for why so many rattan species can co-exist.

The expectation would be that niche-dependent rattan species should be found only in distinct habitats, where soil type, soil moisture, slope exposure, surrounding vegetation and other factors would offer the niche space required by the species. This would suggest that the community of rattans and other plant species has formed by the process of 'niche assembly' (Hubbell, 2001), whereby all available niches are taken, so all niche space is occupied.

Alternatively, if rattan species are neutral and not niche-dependent, they can co-exist within habitats due to ecological equivalence of all individuals. Therefore a community could have arisen by the arrival of various species that co-exist due to lack of mutual competition. The term Hubbell (2001) uses for this process is 'dispersal-assembly'. Such a process may be important in the assembly of rattan species in the Lambusango Forest, since the ideas of island biogeography theory may apply (MacArthur & Wilson, 1967). Following these ideas, Sulawesi can be considered the meta community, providing the primary source of palm species for Buton (Powling, 2009), while Lambusango Forest can be considered the local community, receiving species by dispersal from Sulawesi.

Field observations (Powling *et al.*, 2015) have suggested that some rattans of Lambusango differ in their adaptation to soil pH. Both soil pH and conductivity are quantitative measures of soil differences, likely to be related since both are influenced by the base status of soils. In some situations these parameters can vary over very small distances, for instance when water draining from limestone areas runs over sandstone soils (Powling *et al.*, 2015).

Evidence shows that small-scale variability in soil conditions, particularly soil fertility, influences the distribution of neotropical palms in forests (Svenning, 2001). Soil type can be regarded as a niche parameter and it has been shown that soil nutrient availability influences the composition of understorey palm communities in Panama (Andersen *et al.*, 2012). Transplantation experiments have shown that species which occur naturally in low-nutrient sites grow better in such sites, compared with species which occur naturally in high-nutrient sites. To some extent the relative performances of the species were reversed in high-nutrient sites (Andersen *et al*., 2014).

The work to be described concerns an investigation of soil parameters and their influence on the diversity and distribution of rattan species at various sites, with differing geology, in Lambusango Forest. The sites were separated by distances of up to 12 kilometres and were deliberately chosen for their variety of rock and soil types. Thus the survey took place over a wider area and in a wider variety of habitats than most, if not all, published surveys designed to test the neutral theory of biodiversity (Chase, 2014). Soil pH and conductivity, together with canopy cover, tree number and tree trunk area, were measured in quadrats at the sites. This paper describes only the influence of soils on rattans, since soil type was found to be the primary factor controlling rattan species diversity. However, other factors can influence rattan growth and diversity and soil characteristics are not the sole influence.

It can be assumed that conductivity is an approximate measure of soil fertility, with increasing conductivity indicating increasing fertility. However, the possibility of toxic or non-nutrient ions being present in some soils, particularly ultrabasic soils, means that such a relationship might not hold. Soil pH, rather than conductivity, is therefore used in some of the following analyses as a better single measure of general soil conditions. Plants vary in their ability to grow on soils with different pH values, with requirements for either alkaline or acid soils shown by some plants (Grime *et al*., 2007). Such plants occupy at least two different edaphic niches when soil pH is taken as a niche axis.

The object of this investigation was to determine whether the congeneric rattans require just one or two distinct soil types or whether they show spaced distributions along axes of soil pH and conductivity, suggesting each species occupies a distinct edaphic niche. Edaphic niches might then explain why at least 20 rattan species co-exist.

## MATERIALS AND METHODS

### Description of forest sites

The study was carried out in the Lambusango Forest on the island of Buton, within both the reserve and the surrounding area, which is officially designated as 'limited production forest'. Together these areas cover 95,000 ha (Widayati & Carlisle, 2012). Outline maps of Buton and the forest are presented in Powling *et al*. (2015). The 'limited production forest' is set aside for low-intensity timber extraction; steep slopes in this area make intensive logging and rattan collection difficult. The main survey of rattan abundances took place during July and August 2010. This period would normally be the dry season, which lasts from July to October. However, due to La Niña weather conditions, arising from inter-annual sea surface temperature variations of the tropical Pacific (NOAA, 2016), heavy rainfall was experienced throughout the study period.

The survey of rattan abundances was conducted at sites in the forest, named Anoa, Bala, Kakenauwe and Lapago, which are shown on the map of the forest in Powling *et al*. (2015). An additional site, Jalan Kodok, lying between Kakenauwe and Lapago, was also used. Sites were chosen which showed little evidence of rattan collection in the years before the survey. They differed in underlying geology (Milsom, 2000) and therefore topographies and soils. Topographies varied from shallow to steep slopes and included ridges and river valleys. The altitudes of the survey sites varied from approximately 250 m to 500 m above sea level. Sites were selected to include soils derived from the following rock types: limestone, sandstone, chert and peridotite; alluvial soils were also included.

### Rattan abundance survey

Rattans were investigated along linear transects which ran through areas of forest with uniform soil types. Six 30 × 10 m quadrats were recorded on each transect, with 30 m gaps between quadrats so that vegetation in each quadrat was independent of that in its neighbours. As a result, the length of a typical transect was 330 m. Between 12 and 24 quadrats were recorded at each forest site, on either two or four transects. There was one exceptional transect, on chert soil at the Bala site, where nine quadrats were recorded over a length of 510 m. An overall total of 87 quadrats on 14 transects were recorded.

Within each quadrat individual plants, and number of stems of multi-stemmed species, of all rattan species were counted. The rattan species had been identified previously by comparison with named specimens in the herbaria at Kew, U.K., and Bogor, Indonesia (Powling, 2009).

### Soil measurements

Soil samples were taken from the centre (15 m) of each quadrat from a depth of 1–5 cm. Soil (15 ml) was mixed with 10 ml of demineralised water and measurements made using a Hanna Combo pH and EC meter (Hanna Instruments, Rhode Island, USA).

Soil moisture at a depth between 1.0 and 6.5 cm was determined in situ as a percentage of the maximum moisture capacity of the soil in question, using a Kelway soil tester (Kel Instruments, New Jersey, USA). The measurements reported were taken on a single day, 8th August 2009.

### Data analysis

Data were analysed using Microsoft Excel 2007 and Minitab 16. Standardized mean difference effect size (d) scores were calculated using the Practical Meta-Analysis Effect Size Calculator program (Wilson, 2013). Other calculations were performed according to Magurran (2004).

## RESULTS

### Species investigated

The rattan species found, their total numbers and the number of quadrats in which each species occurred are shown in Table 1. The Table shows 12 named species, with two entries for the species *Calamus zollingeri*, indicated by the local names for the two varieties 'batang' and 'mombi' (Powling, 2009). Results to be presented show that these two varieties differ significantly in their response to soils of differing pH values, so the two varieties are treated separately, except for the rank-abundance plot and species abundance distribution. Three unidentified species are included in Table 1 since they were also found in the survey. Five other species known to exist in the forest (Powling, 2009) were not found during the survey.

### Competition between rattans

If rattan species segregate into niches on soils of different types it would be expected that they compete for soil resources, *i.e.* show root competition. Fig. 1 shows that quadrats contained between one and eight species, with a modal number of four. The number of individual rattan plants and stems averaged 30.1 per quadrat, with a range between 3 and 102. The 102 individuals occurred in one of the quadrats with eight species. In view of the density of species and individuals in at least some of the quadrats it seems probable that root competition does occur between rattan species.

It was noted that within disturbed habitats there were frequently one or two common or dominant species. These were often *C. zollingeri* (one or other variety) and/or *C. ornatus*, with in one case *Calamus* sp. 2 being most common. These species are multi-stemmed and able to form clumps of stems derived from one original plant, so able to hold their position and spread. The commonness of these species in disturbed areas suggests this characteristic gives them a competitive advantage above ground over other rattans in high light environments.

Table 1. Species of rattan found in survey quadrats

| Rattan species found in survey (as listed in Powling, 2009) | Species no. | No. of Individuals | No. of quadrats |
|---|---|---|---|
| *Calamus koordersianus* Becc. | 1 | 149 | 21 |
| *Calamus leptostachys* Becc. ex K. Heyne | 2 | 132 | 22 |
| *Calamus minahassae* Warb. ex Becc. | 3 | 167 | 47 |
| *Calamus mindorensis* Becc. | 4 | 28 | 9 |
| *Calamus ornatus* Blume | 5 | 561 | 60 |
| *Calamus pedicellatus* Becc. ex Heyne | 6 | 47 | 10 |
| *Calamus siphonospathus* Mart. | 7 | 158 | 25 |
| *Calamus suaveolens* W. J. Baker & J. Dransf. | 8 | 157 | 9 |
| *Calamus subinermis* H. Wendl. ex Becc. | 9 | 18 | 10 |
| *Calamus symphysipus* Mart. | 10 | 102 | 25 |
| *Calamus validus*† W. J. Baker | 11 | 4 | 3 |
| *Calamus zollingeri* Becc. 'batang' | 12 | 96 | 20 |
| *Calamus zollingeri* Becc. 'mombi' | 13 | 440 | 36 |
| *Calamus* sp. 1 | 14 | 354 | 26 |
| *Calamus* sp. 2 | 15 | 193 | 14 |
| *Calamus* sp. 3‡ | 16 | 11 | 3 |

†Previously *Daemonorops robusta* (Baker, 2015).
‡ A species not listed in Powling, 2009.

## Rank-Abundance and Species Abundance Distribution

A rank-abundance (Whittaker) plot (Magurran, 2004) of all species is shown in Fig. 2. The species show an acceptable fit to a linear (geometric) distribution (Kolmogorov-Smirnov test statistic = 0.162 with a 5% critical value = 0.224), which indicates an order of dominance among the species. However, the species curve is noticeably sigmoid. Such a curve shape often results when plotting species found in communities and indicates that the geometric model of species dominance might not apply.

The sigmoid shape suggests the overall species abundance distribution may be lognormal (Magurran, 2004). This distribution results when some species are common and some rare but a larger number are of intermediate occurrence. When logarithms of species numbers are plotted as a histogram a normal distribution results (Preston, 1962). The result for the rattan species is shown in Fig. 3, where logarithms to the base 4 are used (black columns). The distribution expected if the rattans followed an exact lognormal distribution is also plotted (white columns). The observed distribution does not differ significantly from the expected lognormal distribution (Kolmogorov-Smirnov test statistic = 0.143 with a 5% critical value = 0.230).

The veil line (Preston, 1962) is on the extreme left of the distribution, with 0.0015 (in effect, zero) species predicted to be beyond (to the left of) the veil line. This position is to be expected given that the rarest species (*C. validus* and *Calamus* sp. 3) each occurred in three quadrats, when in most lognormal distributions the rarest species occurs in only one quadrat. The position of the veil line would appear to indicate that all the rattan species in the forest were found during the survey. However, this is known not to be the case (Powling, 2009).

## Relationship of soil pH and soil conductivity

Measurements made on soil samples during July and August in 2010 are plotted in Fig. 4. This includes measurements additional to those made on the soils in the 87 quadrats. The Figure shows a U-shaped curve with conductivity initially declining as pH rises, but then increasing to high values as pH increases further. It is presumed that at the lowest pH values certain substances, such as manganese, aluminium, possibly iron and soil organic acids, become ionised and soluble (Grime, 2001), thus contributing to conductivity. Some of these ions, particularly aluminium, may be toxic to many plants, including rattans. Most of the soil samples with the lowest pH values were from the area with chert bedrock and low rattan diversity, where acidity and drought during the dry season may together make conditions impossible for most rattan species.

## Responses of rattan species to soils

The mean values for pH and conductivity of the soils in quadrats in which the rattan species grew are plotted in Fig. 5. It can be seen that the species are distributed in the same general pattern as the soil samples (Fig. 4). This indicates that most, if not all, soil types are exploited by at least one rattan species.

Fig. 6 shows a plot of the mean pH values and ranges of the soils on which the rattan species were found growing (*C. validus* is omitted due to only four plants being recorded in the survey). The plot shows that the species with the broadest ranges have soil pH means between approximately 5.0 and 6.5. Species that are better adapted to soils with higher and lower pH values have narrower ranges. It is noticeable that three species adapted to low pH soils have very small ranges. This indicates that some species are specialised to tolerate acidic soils but cannot grow on soils with higher pH values. To a lesser extent this also applies to species adapted to grow on soils with high pH values. The general relationship is not an artefact caused by small sample size resulting in the appearance of limited range, since there is no significant correlation between sample size and range ($r = 0.389$, $p = 0.152$). However, the three species referred to above are exceptions since they have small ranges even when allowing for their sample size, suggesting that they are specialised for growth only on very acidic soils.

Comparison of species on soils with different pH values could be made by performing a one-way analysis of variance. However, such an analysis would require homogeneity of variances for the species and this was not the case. Even when using only the 12 species and varieties with the largest sample sizes, Bartlett's test statistic was 652.04, $p<0.001$, and Levene's test statistic was 39.08, $p<0.001$. Therefore, to compare the species' abilities to grow on different soils a matrix of d values (Nakagawa & Cuthill, 2007) is presented (Table 2). A d value is a standardised measure of the size of difference and can have 95% confidence limits calculated to show whether the d value indicates a statistically significant difference between two species being compared. The matrix in Table 2 arranges the rattan species in order of their mean soil pH values (four species with low numbers of individuals found in the survey are excluded from the matrix). The results show that most pairs of species show significant differences from each other, indicating that, generally, they grow in soils with differing pH values. The calculation of d values requires the calculation of multiple t values (one for each pair of species); also the distributions of the soil pH values on which each species was growing were not always

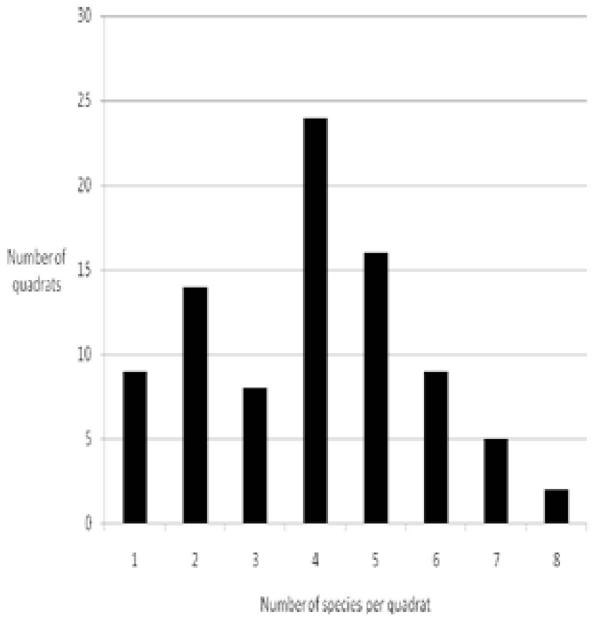

Fig. 1. Distribution of the number of rattan species per quadrat, obtained in the 2010 survey.

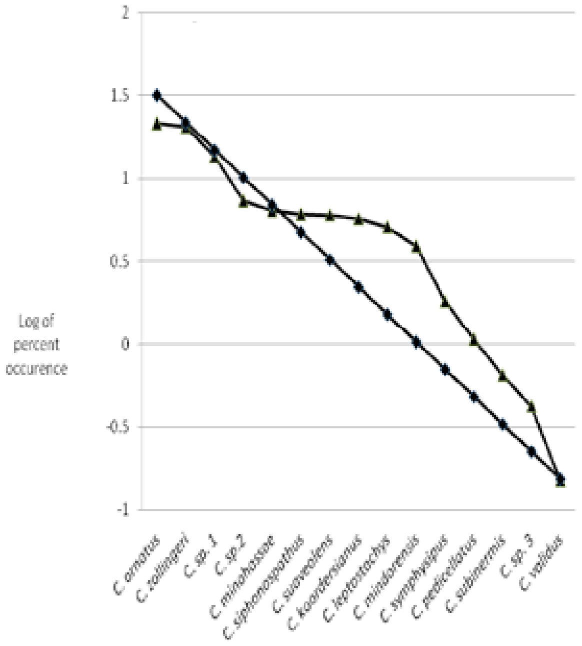

Fig. 2. Rank-Abundance plot for rattan species (triangles) with the fitted line for a geometric distribution (diamonds). The rattan species are ordered on the baseline from most common to least common.

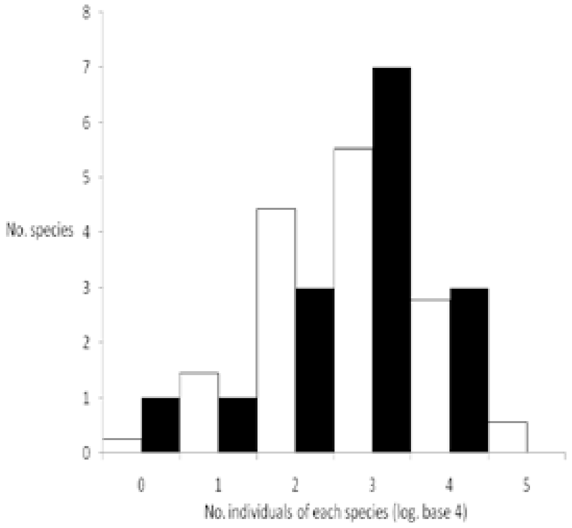

Fig. 3. Species abundance distribution for the rattans. The bars show logarithms (to base 4) of the number of individuals of each rattan species (black columns) and the expected number of species, based on a lognormal distribution, in each category (white columns).

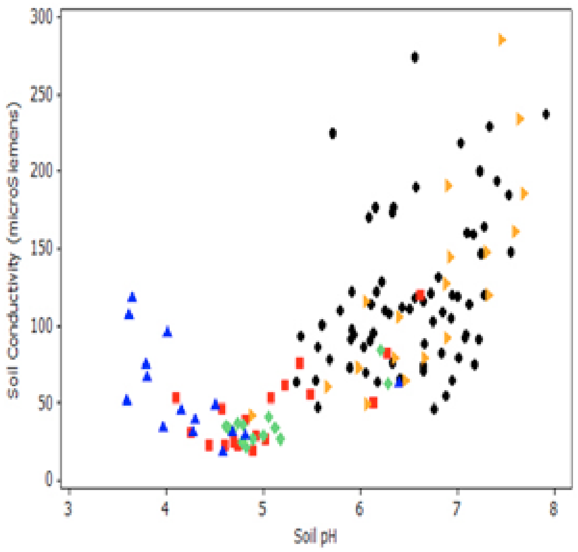

Fig. 4. The relationship between soil pH and soil conductivity. Soil types – black circles: calcareous; red squares: from sandstone; green diamonds: ultrabasic; blue triangles: from chert; orange arrow heads: alluvial.

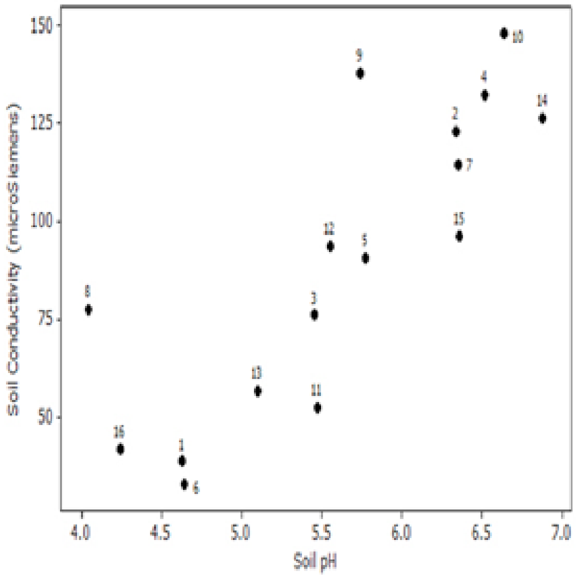

Fig. 5. The relationship between mean values for the conductivity and pH of the soils on which each rattan species was found growing. The species are numbered as in Table 1.

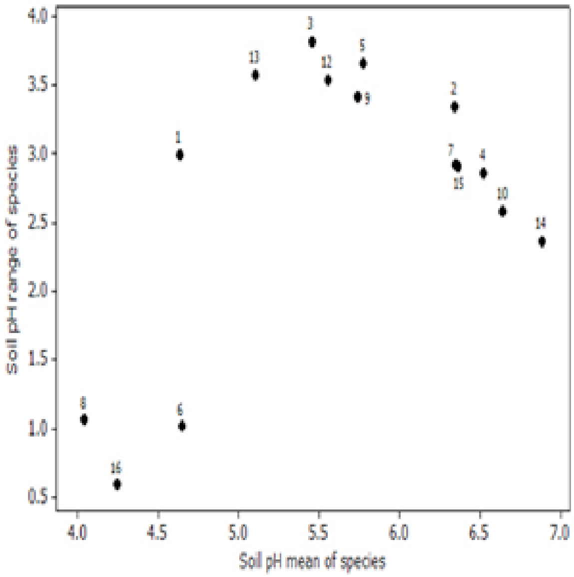

Fig. 6. The relationship between soil pH mean and the soil pH range for the rattan species. *Calamus validus* is omitted due to the low number (4) of individuals found in the survey. The species are numbered as in Table 1.

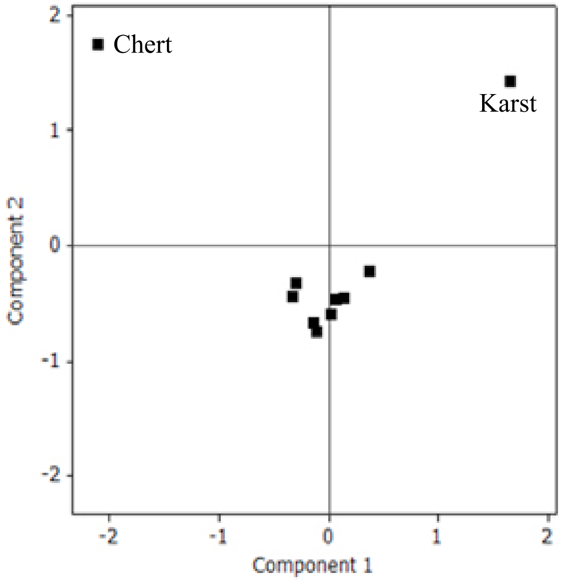

Fig. 7a. Correspondence Analysis. Plot of soil types.

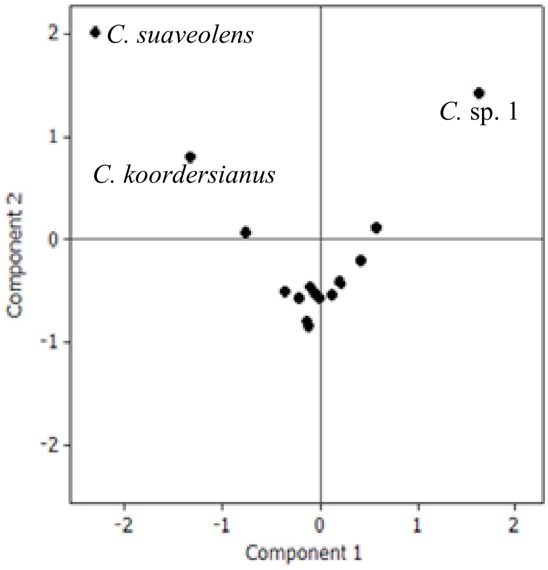

Fig. 7b. Correspondence Analysis. Plot of rattan species.

Table 2. Standardised mean difference effect size (d) scores, with 95% confidence intervals (95% CI) for pairs of species, based on the pH of the soils on which the species grew. The columns for 95% CIs show the lower and upper limits of the intervals. The species pairs that are not significantly different at the 95% level are shown in italics

| Species | *C. suaveolens* | | *C. koordersianus* | | *C. pedicellatus* | | *C. zollingeri* 'mombi' | | *C. minahassae* | | *C. zollingeri* 'batang' | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | d | 95% CI | d | 95% CI | d | 95% CI | d | 95% CI | d | 95% CI | d | 95% CI |
| *Calamus* sp. 1 | 8.72 | 8.15 - 9.28 | 6.14 | 5.71 - 6.57 | 8.75 | 8.07 - 9.42 | 2.64 | 2.45 - 2.83 | 1.72 | 1.51 - 1.93 | 1.72 | 1.47 - 1.97 |
| *C. symphysipus* | 4.20 | 3.76 - 4.64 | 3.21 | 2.83 - 3.58 | 4.27 | 3.68 - 4.87 | 1.94 | 1.70 - 2.19 | 1.40 | 1.13 - 1.67 | 1.35 | 1.04 - 1.66 |
| *Calamus* sp. 2 | 3.51 | 3.18 - 3.85 | 2.59 | 2.30 - 2.87 | 3.72 | 3.26 - 4.18 | 1.36 | 1.17 - 1.54 | 0.95 | 0.73 - 1.17 | 0.92 | 0.67 - 1.18 |
| *C. siphonospathus* | 4.50 | 4.09 - 4.92 | 3.25 | 2.91 - 3.60 | 4.51 | 3.97 - 5.06 | 1.69 | 1.48 - 1.89 | 1.08 | 0.85 - 1.31 | 1.01 | 0.75 - 1.28 |
| *C. leptostachys* | 3.09 | 2.75 - 3.43 | 2.28 | 1.98 - 2.58 | 3.15 | 2.69 - 3.62 | 1.29 | 1.08 - 1.50 | 0.91 | 0.67 - 1.15 | 0.87 | 0.60 - 1.15 |
| *C. ornatus* | 3.72 | 3.46 - 3.98 | 2.31 | 2.09 - 2.53 | 3.51 | 3.15 - 3.87 | 0.76 | 0.63 - 0.89 | 0.34 | 0.16 - 0.51 | 0.26 | 0.04 - 0.47 |
| *C. zollingeri* 'batang' | 2.21 | 1.89 - 2.53 | 1.33 | 1.05 - 1.62 | 1.76 | 1.35 - 2.16 | 0.53 | 0.31 - 0.75 | *0.11* | *-0.14 - 0.37* | | |
| *C. minahassae* | 2.01 | 1.74 - 2.28 | 1.16 | 0.92 - 1.40 | 1.63 | 1.27 - 1.98 | 0.37 | 0.19 - 0.55 | | | | |
| *C. zollingeri* 'mombi' | 2.06 | 1.84 - 2.28 | 0.87 | 0.68 - 1.07 | 1.30 | 0.99 - 1.61 | | | | | | |
| *C. pedicellatus* | 2.54 | 2.14 - 2.95 | *0.05* | *-0.28 - 0.38* | | | | | | | | |
| *C. koordersianus* | 1.90 | 1.63 - 2.17 | | | | | | | | | | |

| Species | *C. ornatus* | | *C. leptostachys* | | *C. siphonospathus* | | *Calamus sp. 2* | | *C. symphysipus* | |
|---|---|---|---|---|---|---|---|---|---|---|
| | d | 95% CI | d | 95% CI | d | 95% CI | d | 95% CI | d | 95% CI |
| *Calamus* sp. 1 | 1.79 | 1.64 - 1.95 | 0.63 | 0.42 - 0.83 | 0.88 | 0.69 - 1.08 | 0.66 | 0.48 - 0.84 | 0.35 | 0.13 - 0.57 |
| *C. symphysipus* | 1.12 | 0.90 - 1.34 | 0.35 | 0.09 - 0.61 | 0.40 | 0.15 - 0.65 | 0.34 | 0.10 - 0.58 | | |
| *Calamus* sp. 2 | 0.64 | 0.48 - 0.81 | *0.02* | *-0.20 - 0.24* | *0.02* | *-0.19 - 0.23* | | | | |
| *C. siphonospathus* | 0.81 | 0.63 - 0.99 | *0.01* | *-0.22 - 0.24* | | | | | | |
| *C. leptostachys* | 0.60 | 0.40 - 0.79 | | | | | | | | |

normal. These considerations mean that the exact 95% confidence limits may be uncertain. If approximate 99.9% confidence intervals are calculated, five more pairs are non-significant. This does not alter the general conclusion that most species pairs show a statistically significant difference in their response to soil pH.

### Soil moisture

Soil conditions were investigated at three sites: Lapago, Jalan Kodok and Kakenauwe. All are areas with limestone bedrock, but Kakenauwe differs from the first two by being an area of karst limestone with thinner soils over free-draining bedrock. Kakenauwe has only one widespread and common species, *Calamus* sp. 1, with other species present only in rare patches of deeper soil. The other two sites both have at least five common species (Lapago: *C. ornatus*, *C.* sp. 1, *C. symphysipus*, *C. siphonospathus*, *C. minahassae*; Jalan Kodok*:* *C. ornatus*, *C. zollingeri* 'batang', *C. minahassae*, *C. symphysipus*, *C. leptostachys*). Measurements of soil pH, conductivity and moisture (Table 3) were made in August 2009, during the dry season nine days after the most recent rain. At this time partial El Niño conditions were developing (NOAA, 2016), so the season was drier than normal. It was found that the three sites differed significantly in their levels of soil moisture, with Kakenauwe having the lowest levels. This was as expected since this site would be anticipated, on the basis of its thin soils and geology, to be the most drought-prone. It also had significantly higher mean values for soil pH and conductivity than the other two sites; however, the individual values did not exceed some of the higher values recorded from the other sites and so cannot be considered lethal for species able to grow in similar conditions elsewhere. The individual quadrat in the survey (on a Jalan Kodok transect) with the highest pH value (7.92) and the third highest conductivity value (237µS) contained seven species of rattan. The deep and moist soil in this quadrat appeared to allow the diversity.

### Correspondence analysis

Correspondence Analysis was used to explore the relationship between soils and rattan species. The soils investigated during the survey were divided into ten different types, based on the sites in the forest where the soils were found. Each soil type was represented by between six and twelve quadrats. These soils differed in their mean pH values, ranging from soil on a chert ridge (mean pH = 4.16) to soil on karst limestone (mean pH = 6.88). The numbers of individual rattan plants or stems of each species on each soil type were used in the analysis. The two main components of variability are presented, with both the soil types and the rattan species plotted (Fig. 7a and 7b). The first component (horizontal axis) represents mainly the pH of the soils. The second component (vertical axis) can be interpreted as mostly re-presenting the moisture content of the soils during the dry season, since the two driest soils (the chert soil and the karst limestone soil) have the highest scores and the lowest scoring is an alluvial soil. The soils themselves mostly cluster together, with the two driest yet furthest apart on the pH scale being quite separate, both from the main cluster and from each other. The plot of the species again shows considerable clustering, suggesting that the requirements of most species are met by the majority of soils that themselves cluster at intermediate pH values and moisture contents. The two most widely outlying species are *C. suaveolens*, which was found only on the chert soil, and *Calamus* sp. 1, found mostly on the karst limestone soil. A few other species distinguish themselves from the cluster of species, showing that they have some adaptation to either dry and acid soils or to dry and calcareous soils.

## DISCUSSION

This work sought evidence for niche segregation among species of rattans, in order to explain how 20 congeneric species can co-exist in the Lambusango Forest. In particular, because observations suggested that different species grew

Table 3. Environmental parameters at sites Lapago, Jalan Kodok and Kakenauwe, August 2009

| | Soil Moisture (% saturation) | | | Soil pH | | | Soil Conductivity (microSiemens) | | |
|---|---|---|---|---|---|---|---|---|---|
| | N | Mean±SD | Stat. popn.† | N | Mean±SD | Stat. popn.† | N | Mean±SD | Stat. popn.† |
| Lapago | 13 | 63.0±9.5 | b | 13 | 6.10±0.58 | b | 13 | 124.5±53.1 | b |
| Jalan Kodok | 17 | 78.1±8.0 | a | 17 | 6.17±0.70 | b | 17 | 158.0±55.9 | b |
| Kakenauwe | 15 | 53.5±4.9 | c | 16 | 6.79±0.50 | a | 16 | 203.8±42.9 | a |

†The different statistical populations to which the measured values belong, as determined by analysis of variance, are indicated by different letters.

on different soil types, evidence was sought for niche separation along axes of soil pH and soil conductivity, these variables being taken as quantitative measures of soil differences. Interspecific root competition would be expected to result in a species well adapted to a particular soil type (its own edaphic niche) out-competing less well adapted species, which in turn prosper on soils to which they are adapted. The co-existence of rattan species in close proximity within 30 × 10 m quadrats (Fig. 1) is circumstantial evidence that root competition occurs. However, the presence of many different species in most quadrats suggests that such competition is not strong.

A rank-abundance plot (Fig. 2) of the species found during the survey gave a sigmoidal curve and when log transformed the species abundance distribution (Fig. 3) was not significantly different from a lognormal distribution. This is a commonly observed relationship (Magurran, 2004). The veil line at the extreme left of the distribution should indicate that all rattan species in the forest had been found in the survey. However, previous work (Powling, 2009) has shown that at least five other species exist there, but these were not found in 2010 due to their rarity and the relatively small size of the survey.

A species abundance distribution with the general shape of a lognormal distribution can arise due to either competitive (niche) or dispersal (neutral) processes. A lognormal distribution arises if communal niche space is sequentially subdivided into niches occupied by species (Sugihara, 1980). Alternatively, if constant immigration from a meta community into a local community occurs the local community will remain stocked with species despite species losses due to random extinctions, again resulting in an approximately lognormal distribution (Loreau and Mouquet, 1999). Thus the species abundance distribution observed for the rattans does not show whether the community is a result of niche assembly or dispersal assembly.

It was found that the U-shaped pattern obtained in the dot plot of soil conductivity *vs*. soil pH (Fig. 4) was reflected in the plot of the means of the species on the same axes (Fig. 5). This indicates that soil preference results from adaptations involving trade-offs, so is mostly controlled genetically, and that species occupy different niches on axes of soil pH and conductivity. The spaced distributions on the axes suggest that adaptation to different soils may have been a major factor in *Calamus* speciation.

The plot of pH range *vs*. pH mean (Fig. 6) shows that some species, those with intermediate values for pH mean and wide ranges, can be considered generalists, whilst those with more extreme pH means and smaller ranges are more specialised. Again this indicates that genetic differences between species are responsible for the differences they show in their abilities to grow on soils of different types. However, the wide ranges show that although many rattan species may prefer soils of a particular pH they are by no means limited to such soils and can grow on a variety of other ones. The conclusion might be that, even if the species show niche structure along a soil pH gradient, many species occupy broad niches and that interspecific competition may be weak.

An attempt was made to quantify the differences between the species. Analysis of variance was not used since the variances of the variables (the pH values of the soils on which the rattans were growing) were not homogeneous. This was anticipated since there is no theoretical reason to expect niches for species along an axis to be equal in size. Instead, Standardised Mean Difference (d) values (Nakagawa & Cuthill, 2007) were calculated for each pair of species, together with the 95% confidence intervals for the d values (Table 2). All except five pairs of species showed significant differences at approximately the 95% level.

Since statistical difference cannot be assumed to indicate biological difference the result cannot be taken to indicate that any particular pair of species do or do not occupy the same edaphic niche, given the absence of a theoretical expectation of how big a difference would indicate separate niches. Indeed, species' niches can be very close together on an axis, with the species co-existing for long periods of time (Scheffer & van Nes, 2006). Nevertheless, the considerable differences between most species pairs (high d values) suggest that many rattan species do occupy different edaphic niches.

The species pairs that are not statistically different show that some species have similar preferences for soil pH. In these cases competition between the species in the pairs may be avoided if they differ from each other along one or more other (unmeasured) niche axes and so do not normally grow together. One example of this may be *C. siphonospathus* and *Calamus* sp. 2, which were never found growing together. Other pairs consisted of species which were found together at one or more sites. A possible explanation for the co-existence of such species in the forest is that one of the pair may have a narrow range of soil pH tolerance, *i.e*. a narrow niche, and the other have a wider range, a broad niche. An example is *C. pedicellatus* (narrow range) and *C. koordersianus* (wide range). Another pair that co-exist at many sites is *C. zollingeri* 'batang' and *C. minahassae*, with the first species often found in more open vegetation than the second. Thus competition between the species in these pairs may occur at some but not all sites, so be insufficient for one species to competitively exclude the other from the forest.

The measurements of soil moisture, pH and conductivity made in the relatively dry conditions of August 2009 (Table 3) show that soils at different sites differ significantly in soil moisture as well as in pH and conductivity, at least during the dry season which occurs in most years (Powling *et al*., 2015). A lack of soil moisture at a site might be expected to influence which species are capable of surviving there, and the site with the lowest soil moisture, Kakenauwe, lacks most species, only one species, *Calamus*. sp. 1, being common.

The correspondence analysis (Fig. 7a & 7b) shows the soils separated by the reaction of the species to them and the species separated by their reaction to the soils. The horizontal axis can be categorised as mainly registering the influence of soil pH. The vertical axis seems to mostly register the influence of soil moisture, with some species showing segregation along it. Segregation into hydrological niches is widespread among plants (Silvertown *et al*., 2015). Due to La Niña rains and saturated soils, no direct evidence for hydrological niches could be collected during the 2010 survey. However, the results in Fig. 7a & 7b and Table 3 suggest that hydrological niches influence rattan diversity.

Two species stand out in the plot of the species (Fig. 7b). *Calamus suaveolens* was found only on the chert ridge and is associated with this site in the correspondence analysis, whilst *Calamus* sp. 1 was found predominantly on the karst limestone at Kakenauwe and is likewise associated with this site. The main feature of the results is the clustering of most of the soils and most of the species. It appears that most species do not distinguish between the soils which have intermediate pH values (5.0 to 6.5) and retain high levels of soil moisture throughout the year. It could be that the correspondence analysis lacks the resolution to differentiate the majority of species, given that this work has shown that most species are distinct from each other in their reaction to soil pH (Fig. 6, Table 2). Nevertheless, it seems that many species are able to grow on a wide range of soils, due to the wide tolerance of soil pH variability that they show. Again, this suggests there is little competition on these intermediate soils. Perhaps roots of rattan species have to compete more with tree roots than among themselves.

This work has produced evidence that rattan species have distinct soil preferences related to pH and conductivity. This can be taken as evidence of edaphic niches, although the degree of separation between species required for niches to be assumed has not been established. It is a common observation that many plants show requirements or preferences for soils with particular pH values (Grime *et al*., 2007) and the work described here demonstrates this observation for congeneric rattans. Some species are found on acidic soils and seem to be limited to such soils (*C. suaveolens, C. pedicellatus, Calamus.* sp. 3), one species shows a distinct preference for calcareous soils (*Calamus*. sp. 1). However, most species, although they have a preferred soil pH optimum, are able to grow on a wide range of soils, so sites with soils of intermediate pH typically have many different species of rattan present.

Matthews and Whittaker (2014) divide neutral theory into two forms, hard and weak neutrality. These authors state that weak neutrality applies when neutral (“null”) models “moderately explain community structure, even if fine scale examination reveals that species do differ in their niche characteristics”. Weak neutrality theory may have some relevance to the rattans in Lambusango Forest in that, although there is evidence that species occupy edaphic niches, there is considerable overlap of the niches and little evidence for competitive exclusion of species from sites with soils of intermediate pH. Therefore, many species appear to be ecologically equivalent. These considerations only apply to edaphic niches and root competition; it may be that other factors (other niche axes) also influence the species and prevent competition eliminating species from many situations.

The possibility that neutral processes may influence the rattans in Lambusango Forest leads to consideration of the maintenance of rattan diversity there. Neutrality implies that dispersal of species is important in maintaining plant diversity (Condit *et al*., 2012), the dispersal of rattans being through the agency of birds such as frugivorous pigeons and hornbills (Zona & Henderson, 1989) known to be present on Buton (Martin *et al*., 2012). The source of rattan species would mostly be the far larger island of Sulawesi to the north, which can be considered to hold the meta community; the dispersal path being from south east Sulawesi *via* northern Buton to the forest in southern Buton. A path through Muna, the island immediately to the west of Buton, is unlikely at present since Muna has been largely cleared of natural vegetation to convert the ground to agricultural production. The path from northern Buton is still possible due to the presence of more or less continuous forest from north to south. The danger is that the path becomes difficult in future due to loss of forest, so dispersal into Lambusango Forest is diminished and the diversity of rattans declines.

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