Species limits, geographical distribution and genetic diversity in *Johannesteijsmannia* (Arecaaceae)

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Four species are recognized in the understorey palm genus *Johannesteijsmannia* (Arecaaceae), all of which occur in close geographical proximity in the Malay Peninsula. We hypothesize that overlapping distributions are maintained by a lack of gene flow among species and that segregation along morphological trait or environmental axes confers ecological divergence and, hence, defines species limits. Although some species have sympatric distributions, differentiation was detected among species in morphological and genetic data, corroborating current species delimitation. Differences in niche breadth were not found to explain the overlapping distribution and coexistence of *Johannesteijsmannia* spp. Four species formed over the last 3 Mya, showing that diversity accumulated within a short time frame and wide range expansion has not occurred, potentially due to a lack of time for dispersal or the evolution of traits to facilitate movement. An assessment of genetic diversity is presented and, as expected, the widest distribution in the genus harbours the highest genetic diversity. © 2016 The Linnean Society of London, Botanical Journal of the Linnean Society, 2016


INTRODUCTION

‘As species of the same genus have usually, although by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus when they come into competition with each other than between species of distinct genera’ (Darwin, 1859, p. 76).

For more than a century (Darwin, 1859; Bates, 1863; Wallace, 1865), biologists have been interested in where species are distributed and how closely related taxa can co–occur in geographical space (e.g. Huey & Pianka, 1977; Dietrich & Wehner, 2003; Ley & Hardy, 2014). Co-occurrence of closely related species can result from secondary contact of taxa that originated allopatrically, which is the evolution of reproductive isolation as a function of geographical isolation, or in the absence of geographical barriers through sympatric speciation, although convincing examples remain few (Coyne & Orr, 2004). Although phylogenetic niche conservatism (Blomberg & Garland, 2002) predicts higher ecological similarity between closely related species as a result of their retention of ancestral traits (Losos, 2008), resource...
partitioning is often a requirement for competing species to coexist (MacArthur, 1972). Regardless of the speciation mechanisms driving species origination, closely related species that are sympatric are maintained in the same local geographical area by partitioning space, whether it is on one or multiple axes of that space, such as for genetic, morphological or niche traits.

Species diversification can result from the exploitation of new ecological resources (Simpson, 1944; Schluter, 2000) and ecological divergence can play a fundamental role in the reproductive isolation of species (e.g. Schluter & Conte, 2009; Papadopoulos et al., 2014). In a study comparing species pairs, Funk, Nosil & Etges (2006) found a significant positive relationship between ecological divergence and reproductive isolation, showing that closely related and co-occurring species are expected to have some degree of environmental divergence. Species that have overlapping distributions across geographical space present similarity their climatic requirements, at least at a coarse scale, but may differ in other components that drive ecological divergence, such as pollination biology (Johnson, 2006; Van der Niet, Peakall & Johnson, 2014; Restrepo et al., 2016, this issue).

A notable case of ecological divergence among sympatric species was described in *Howea* Becc. (Arecales), in which sister species maintain their sympatric distributions on Lord Howe Island by partitioning morphological and ecological niche space (Savolainen et al., 2006). These sister species exhibit distinct phenological traits and flowering time only slightly overlaps, thus inhibiting pollen transfer and gene flow. Niche space also differs where distributions are dependent on local variation in soil acidity. Remarkably, ecological isolation has been shown to drive divergence in sympathy in other congeneric species groups in the flora of this small island (Papadopoulos et al., 2014).

At a finer taxonomic scale, cases of resource partitioning among sympatric South American species of *Geonoma* Willd. (Arecales) have been identified. One study showed distinct phenological patterns and staggered flowering times among sympatric varieties of *G. cuneata* H.Wendl. ex Spruce (Borchsenius, 2002). Minimal temporal overlap in flowering was sufficient to avoid competition among the four varieties examined, even when pollinator guilds and other aspects of pollination ecology were not markedly different. Another suite of pollination ecology studies showed that when flowering times are shared among sympatric congeners or even varieties of one species, floral scent composition partitions resources to distinct pollinators and allows for reproductive isolation (Knudsen, 1999, 2002; Borchsenius, Lozada & Knudsen, 2016; this issue). Furthermore, habitat differentiation is suggested to maintain the co-existence of sympatric varieties of *G. macrostachys* Mart. (Roncal, 2006), with one variety occurring in floodplains and the other in adjacent and interspersed in *terra firme* forests with different constituent soil characteristics. As well evidenced from the preceding examples, palms are excellent models for the study of evolution and phylogeography of tropical forests (Bacon, 2013; Couvreur & Baker, 2013).

Of all tropical rainforest regions, Southeast Asia is one of the most geologically dynamic owing to the combination of collision and reorganization of tectonic plates, high levels of volcanic activity and repeated fluctuations in sea level (Morley, 2000; Hall, 2009). These abiotic factors have led to habitat fragmentation and dispersal, and have been suggested to foster high rates of speciation (e.g. Esselstyn, Timm & Brown, 2009; Bacon et al., 2013). Biotic diversification in Southeast Asia is associated with some of the highest rates of endemism on the planet, resulting in globally important biodiversity hotspots (Myers et al., 2000). More specifically, Malaya (Fig. 1A), or the area between the Isthmus of Kra at the border between Myanmar and Thailand, to New Guinea (Dransfield, 1987), is extremely diverse, containing >1000 palm species in >50 genera (Dransfield et al., 2008) and is regarded as the greatest palm diversity hotspot in the world (Baker & Couvreur, 2013a).

Within this rich Southeast Asian palm diversity, *Johannesteijsmannia* H.E. Moore presents an interesting phylogeographic pattern of species co-occurrence. *Johannesteijsmannia* is a genus of four species of spectacular, understory fan palms belonging to subtribe Livistoninae (Trachycarpeae: Coryphoideae; Bacon, Baker & Simmons, 2012). The species are West Malayan, ranging from southern Thailand, Peninsular Malaysia and Sumatra to western Borneo (Fig. 1). Only one species [*J. altifrons* (Rchb.f. Zoll.) H.E.Moore] is widespread throughout this part of Southeast Asia; the other three species are endemic to Peninsular Malaysia (Dransfield, 1972). All four species are found in Peninsular Malaysia (Look, 2007), which comprises an area of c. 131,000 km². Some species are found in adjacent sites and form overlapping, parapatric or adjacent distributions and others occur sympatrically within the same site. For example, *J. lanceolata* J.Dransf. and *J. magnifica* J.Dransf. grow side by side with *J. altifrons* in the Sungai Lalang forest reserve (Chan, Chua & Saw, 2012). This pattern of co-occurrence among congeners prompts the following questions: (1) Are the species currently recognized in *Johannesteijsmannia* truly distinct? (2) What is the genetic diversity of populations and species? and (3)
Can evolutionary and ecological processes be identified that led to or maintain co-occurrence among species? High levels of sympatry among congeners are not uncommon in tropical forests (e.g. African Marantaceae; Ley & Hardy, 2014), in Southeast Asia (Gower et al., 2012) or even in the palm family (Baker & Couvreur, 2013b). For example, field observations indicate that multiple species of *Calamus* L., *Licuala* Wurmb and *Pinanga* Blume (Arecaceae) co-occur in the same area of Southeast Asia (Dransfield et al., 2008).

Here, we address the three questions above by investigating the phylogeographical history of *Johannesteijsmannia*. We measured morphological traits and genetic diversity of multiple populations of all *Johannesteijsmannia* spp. The genetic structure, climatic niches and a multilocus coalescent species tree were estimated to infer the ecological and genetic relationships among populations and described species. Findings from this study may contribute to a more general understanding of co-occurrence in tropical florals.

**MATERIAL AND METHODS**

**Population sampling**

For phylogeographic analysis, 221 individuals were collected from 27 populations of the four currently recognized species (Fig. 1; Appendix 1). Field
sampling covered the entire geographical range of *Johannesteijsmannia*, except for the Sumatran populations, which were inaccessible at the time of sample collection.

**Morphometrics**

To test species limits, overlapping morphologies and the potential for gene flow among populations, 11 morphological characters were compiled from 203 accessions (Appendix 2; 18 individuals collected for the phylogeographic analysis did not have all characters present for scoring). Multivariate analysis of morphological data can be advantageous because it does not require a priori hypotheses of groups or species delimitations. This approach has been demonstrated to be a powerful method for testing species concepts in other palm groups (Loo et al., 2001; Henderson, 2002; Henderson & Ferreira, 2002; Henderson, 2004, 2006). Principal coordinates analysis (PCoA) using Gower's general similarity coefficient (Gower, 1971) was performed as it has been shown to be appropriate for mixed datasets of qualitative and quantitative characters (Legendre & Legendre, 1983).

**Amplified fragment length polymorphisms (AFLPs)**

We used AFLPs (Vos et al., 1995) to determine if populations of putative *Johannesteijsmannia* species presented evidence of hybridization or gene flow. Although AFLP data are limited by their co-dominant nature and the difficulty of identifying homologous alleles, the data are inexpensive to generate and have proved useful in numerous palm studies (e.g. Bacon & Bailey, 2006; Savolainen et al., 2006).

Fresh leaf material frozen in liquid nitrogen was used for DNA extractions (Murray & Thompson, 1980). Genomic DNA was digested with EcoRI and *Mse*I (New England BioLabs) and ligated to double-stranded adaptors. Pre-selective and selective primers were based on adapter primer core sequences (EcoRI CTCTAGAGCTGAGC and AATTGGACGCAGATCT; *Mse*I GACGATGAGTCCTGAG and TACTCAAGGACTCAT) and selective primer combinations (EcoRI-AAG/MseI-CAC, EcoRI-ACA/MseI-CAG, EcoRI-ACT/MseI-CAT, EcoRI-AGC/MseI-CTG, EcoRI-AGG/MseI-CA and EcoRI-AGC/MseI-CAC) were used. Labelled products with internal size standards (GeneScan-500 TAMRA, Applied Biosystems) were analysed on an ABI Prism 377 sequencer (Applied Biosystems).

GeneScan 3.1 (Applied Biosystems) was used to normalize and size fragments, and Genotyper 2.0 (Applied Biosystems) was used to compare all samples, define loci, and output the data matrices for subsequent analyses. A locus was defined as any single fragment with minimum amplitude of 50 fluorescence units occurring in at least one accession. Loci were scored between 50 and 400 bp. All samples were scored for the absence or presence of an allele at each locus; pairs of loci with overlapping positions were discarded.

**Genetic diversity**

To examine genetic diversity the Shannon information index (*I*) was estimated in POPGENE 1.31 (Yeh, Yang & Boyle, 1999). The *I* index was chosen because it does not take shared absence as an indication of similarity (e.g. Dawson et al., 1995). In addition, analysis of molecular variance (AMOVA; Excoffier, Smouse & Quattro, 1992) was performed in ARLEQUIN 2.0 (Schneider, Roessli & Excoffier, 2000) where the total genetic diversity was partitioned between species, between populations within species and between individuals within populations. For each species, the total genetic diversity was partitioned between populations and between individuals within populations. The variance components were used to compute fixation indices (Wright, 1965) and the significance of the indices was tested non-parametrically (Excoffier et al., 1992) using 10 000 permutations.

**Population structure**

To test for the presence of intermediates between *Johannesteijsmannia* spp., AFLP data were analysed using population assignment tests (Structure v2.3.2; Pritchard, Stephens & Donnelly, 2000). Structure minimizes the deviation from Hardy-Weinberg and linkage equilibria within each putative cluster by the fractional assignment of individual genomes to *K* populations. The admixture model was implemented with correlated allele frequencies and without the use of a priori information from populations of origin. Simulations included three iterations for *K* = 1–10, with a 100 000 generation burn-in and 200 000 chain length. The most probable number of genetically homogeneous groups (*K*) was determined by the Δ*K* statistical procedure (Evanno, Regnaut & Goude, 2005) as implemented in Structure Harvester v0.6 (Earl & Vonholdt, 2012).

**Coalescent species tree**

Two hundred and four clones of three or four individuals per species were sequenced (Appendix 3) for two low-copy nuclear genes, PRK and RPB2 (Lewis & Doyle, 2002; Roncal et al., 2005). Nucleotide alignments were obtained independently for each of the two loci using default parameters in MUSCLE (Edgar, 2004) as performed in Geneious R6 (Biomatters, 2013). The species tree was inferred using
BEAST in BEAST 1.7.5 (Heled & Drummond, 2010). The analysis was run using a calibrated Yule species tree prior (Heled & Drummond, 2012) and the GTR+Γ model of nucleotide substitution with four gamma categories. Markov chains were sampled for 100 million generations and repeated three times to test for convergence and to ensure effective sample sizes (ESS) exceeded 200. Burn-in was determined in Tracer 1.5 (Rambaut & Drummond, 2007) based on ESS and parameter trajectories and was removed in LogCombiner 1.7.5.

TIME SINCE ORIGIN
We compared diversification rates in Johannesteijsmannia with those of all other palm genera. Despite the disadvantage of incorporating a negligible extinction rate in the birth–death model, we estimated diversification rates following Magallón & Sanderson (2001) because of its simple and non-parametric approach. Using dated phylogenetic trees for the entire palm family (Baker & Couvreur, 2013a, b) and Livistoniae (Bacon et al., 2013), we examined all node ages of palm genera that originated during the last 10 million years (My) for the number of species as listed on the online palm biodiversity information portal, Palmweb (Palmweb, 2016).

CLIMATIC NICHE
To build environmental niche models for each Johannesteijsmannia sp., we used georeferences from all collection localities and additional localities that were manually verified based on personal observation that were obtained from the Global Biodiversity Information Facility database (http://www.gbif.org/occurrence), the herbarium at the Royal Botanic Gardens, Kew, and the monograph of the genus (Dransfield, 1972; Appendix 1).

To reduce redundancy among the variables we generated correlation matrices for all WorldClim variables with a resolution of 1 km² (Hijmans et al., 2005) in R 3.0.2 (R Development Team, 2008). We defined a minimum correlation threshold at 0.75 and discarded one random variable from each pair with a correlation higher the threshold. The 19 bioclimatic variables were reduced to six (mean diurnal temperature range, isothermality, temperature seasonality, precipitation of the driest month, precipitation of the wettest quarter, precipitation of the warmest quarter). Candidate models for each species were constructed using the maximum entropy algorithm (Maxent; Phillips, Dudik & Schapire, 2004) using three different parameter settings: (1) with default parameters; (2) without hinge and threshold features; and (3) only with linear features. Each setting was run with two values of the regularization multiplier (1 or 3) for a total of six candidate models that ran for 30 replicate runs each. Final number of replicates per species varied (see Table S1), depending on the initial sample size. To assess the relative importance of the predictor variables we also generated response curves and performed jackknife analyses. We used the area under the curve (AUC) scores to measure the predictive ability of the model, which approach 1.0 when the model predictions are different from random (no association between environmental variables and occurrence data) and are generally accepted as the best measure for evaluating model performance (Phillips et al., 2004; Elith et al., 2006). The best model out of the six candidates was chosen based on a combination of AUC scores, homogeneity in the use of predictor variables as determined by the response curves and the results of the jackknife analysis.

We compared environmental niches between species by calculating the I and Schoener’s D statistics following Broenniman et al. (2012), which applies a kernel density function to determine the probability of occurrence of each species in environmental space and calculates niche overlap independently of geographical space. To visualize better whether there were appreciable differences in the climatic niche between species, we used the first two axes from a principal component analysis (PCA) summarizing the variation contained in the complete set of bioclimatic variables. We indicate a confidence interval of 90% around our results using ellipses generated by the function oriel-lipse in the R package vegan (Okasanen et al., 2011).

RESULTS
MORPHOMETRICS
The PCoA revealed four distinct groupings (Fig. 2), where axis 1 represented 21% of the total variation and axis 2 represented 13%. The sampled J. altifrons and J. magnifica individuals clustered adjacent to each other and the remaining two species formed more distant groupings. These relationships reflect their distinctive morphology, such as the above ground stem of J. perakensis J.Dransf., which is different from the acaulescent form of the other species, and the narrow leaf shape of J. lanceolata (Appendix 2). Little divergence of character space is noted between J. magnifica populations sampled in Peninsular Malaysia and Borneo.

GENETIC DIVERSITY
The mean number of AFLP fragments per individual was 83, of which 98% were polymorphic. The
percentage of polymorphic loci for each species ranged from 27% (J. magnifica) to 75% (J. altifrons). The Shannon information index ranged from 0.0677 to 0.2355, showing moderate levels of genetic diversity that did not vary significantly (Table 1). The Structure results revealed that there was no admixture among individuals of the different species. All three iterations resolved four independent groups of individuals, corresponding to the four recognized species (Table 2).

**COALESCENT SPECIES TREE**

We explicitly modelled incomplete lineage sorting through the use of a multispecies coalescent tree (Fig. 3). The topology did not have any mutually well-supported conflicts (≥ 75%) with previous hypotheses of species relationships (Bacon et al., 2013). The poorly supported difference in the position of the root of *Johannesteijsmannia* here, as compared to Bacon et al. (2013) may be due to incomplete lineage sorting, so the results shown here are considered to be more accurate because *BEAST accounts for bias that may be introduced from the retention of ancestral polymorphism. *Johannesteijsmannia altifrons* is inferred as the sister of *J. perakensis*, which together are sister to *J. lanceolata*; the three are sister to *J. magnifica*.

![Figure 3. Coalescent species tree inferring the relationships among *Johannesteijsmannia* spp.; posterior probabilities are displayed above branches.](image)

**TIME OF ORIGIN**

*Johannesteijsmannia* was found to have relatively high diversification rates, where four distinct species have originated over the last c. 4 My, resulting in a diversification rate of 0.06–0.14 species per My (Magallón & Sanderson, 2001). When comparing *Johannesteijsmannia* with all other palm genera < 10 My old (Baker & Couvreur, 2013a,b), the genus has a high diversification rate (Table 3).

**Table 1. Genetic diversity of *Johannesteijsmannia* OTUs**

<table>
<thead>
<tr>
<th>Species</th>
<th>P (%)</th>
<th>Mean</th>
<th>I</th>
<th>Ht</th>
</tr>
</thead>
<tbody>
<tr>
<td>J. altifrons</td>
<td>216 (75)</td>
<td>84.5</td>
<td>0.1989</td>
<td>0.1513</td>
</tr>
<tr>
<td>J. lanceolata</td>
<td>172 (59.7)</td>
<td>78.5</td>
<td>0.1395</td>
<td>0.1729</td>
</tr>
<tr>
<td>J. magnifica</td>
<td>77 (26.7)</td>
<td>84.4</td>
<td>0.1068</td>
<td>0.0964</td>
</tr>
<tr>
<td>J. perakensis</td>
<td>88 (30.6)</td>
<td>80.1</td>
<td>0.1138</td>
<td>0.1024</td>
</tr>
</tbody>
</table>

Number of polymorphic loci (P), Shannon Information Index (I) and total genetic diversity (Ht) for each *Johannesteijsmannia* sp.

Environmental niche models showed average AUC scores > 0.85 (Fig. S1; Table S1). Because our AUC results are based on background data and not records of species absence (Lobo, Jiménez-Valverde & Real, 2008), we must interpret our results with some caution. Further, some results, particularly those for *J. lanceolata*, are based on a small sample size (six records total). The niche model of *J. altifrons* had a high relative contribution from the level of precipitation of the driest month, whereas for *J. lanceolata*, precipitation of the wettest quarter had the largest influence on the niche model. For *J. magnifica* and *J. perakensis* mean diurnal temperature was the most important variable in the model (Supporting Information, Table S1). Of the three model types we ran across all four species, the model that implemented the default parameters and a regularization multiplier set to 1 (Model 1A) generated the highest response and, by extension, the most influence from the six climatic variables used after eliminating correlation (Supporting Information, Table S2).

Niche similarity statistics indicate that environmental niches among the four *Johannesteijsmannia* spp. are largely overlapping, even when the most conservative estimate of similarity is considered (Table 4). Together, the first two principal components of the six WorldClim variables explained 95.7% of the total variation in data. PC1 was primarily influenced by precipitation of the wettest quarter (loading 0.972), whereas PC2 primarily represented temperature seasonality (loading 0.725). In accordance with the niche similarity statistics, the climatic space inferred from the PCA shows a region occupied by all four species (Fig. 4), where *J. altifrons* occupies a wider niche space and the other species present narrower niche spaces with only slight differentiation between them.

Differences in elevation were not significantly different from each other based on an ANOVA ($P = 0.519$). There were gross similarities in mean

### Table 3. Time since origin (in million of years, My) and the number of species generated for palm genera <$ 10$ My old

<table>
<thead>
<tr>
<th>Genus</th>
<th>Stem node age</th>
<th>Number of species</th>
<th>Diversification rate [log(n)/t]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthophoenix</td>
<td>4.8</td>
<td>3</td>
<td>0.10</td>
</tr>
<tr>
<td>Acocorhaphae</td>
<td>9.9 (8.96)</td>
<td>1</td>
<td>0.00 (0.00)</td>
</tr>
<tr>
<td>Actinokentia</td>
<td>9.9</td>
<td>2</td>
<td>0.03</td>
</tr>
<tr>
<td>Archontophoenix</td>
<td>9.2</td>
<td>6</td>
<td>0.08</td>
</tr>
<tr>
<td>Balaka</td>
<td>5.5</td>
<td>12</td>
<td>0.20</td>
</tr>
<tr>
<td>Brassiophoenix</td>
<td>7.5</td>
<td>2</td>
<td>0.04</td>
</tr>
<tr>
<td>Barretiokentia</td>
<td>7.6</td>
<td>5</td>
<td>0.09</td>
</tr>
<tr>
<td>Butia</td>
<td>5.2</td>
<td>22</td>
<td>0.26</td>
</tr>
<tr>
<td>Calyptrone</td>
<td>8.3</td>
<td>17</td>
<td>0.15</td>
</tr>
<tr>
<td>Calyptronoma</td>
<td>8.3</td>
<td>3</td>
<td>0.06</td>
</tr>
<tr>
<td>Carpentaria</td>
<td>5.8</td>
<td>1</td>
<td>0.00</td>
</tr>
<tr>
<td>Chambevryonia</td>
<td>4.5</td>
<td>2</td>
<td>0.07</td>
</tr>
<tr>
<td>Coccothrinax</td>
<td>10</td>
<td>2</td>
<td>0.03</td>
</tr>
<tr>
<td>Cyphosperma</td>
<td>9.4</td>
<td>5</td>
<td>0.07</td>
</tr>
<tr>
<td>Cyphophoenix</td>
<td>7.6</td>
<td>4</td>
<td>0.08</td>
</tr>
<tr>
<td>Drymophileus</td>
<td>7.5</td>
<td>3</td>
<td>0.06</td>
</tr>
<tr>
<td>Guithia</td>
<td>7.7</td>
<td>2</td>
<td>0.04</td>
</tr>
<tr>
<td>Hedycepe</td>
<td>9.4</td>
<td>1</td>
<td>0.00</td>
</tr>
<tr>
<td>Hemithrinx</td>
<td>7.2</td>
<td>3</td>
<td>0.07</td>
</tr>
<tr>
<td>Howeia</td>
<td>8.6</td>
<td>2</td>
<td>0.04</td>
</tr>
<tr>
<td>Johannesteijsmannia</td>
<td>10.09 (4.19)</td>
<td>4</td>
<td>0.06 (0.14)</td>
</tr>
<tr>
<td>Jubaee</td>
<td>5.2</td>
<td>1</td>
<td>0.00</td>
</tr>
<tr>
<td>Kentiopsis</td>
<td>4.4</td>
<td>4</td>
<td>0.14</td>
</tr>
<tr>
<td>Kerriodoxa</td>
<td>8.9</td>
<td>1</td>
<td>0.00</td>
</tr>
<tr>
<td>Laccospadix</td>
<td>8.6</td>
<td>1</td>
<td>0.00</td>
</tr>
<tr>
<td>Lanonia</td>
<td>X (8.63)</td>
<td>8</td>
<td>X (0.10)</td>
</tr>
<tr>
<td>Leucothrinax</td>
<td>7.2</td>
<td>1</td>
<td>0.00</td>
</tr>
<tr>
<td>Lytocaryum</td>
<td>8.54</td>
<td>4</td>
<td>0.07</td>
</tr>
<tr>
<td>Normanbya</td>
<td>8.1</td>
<td>1</td>
<td>0.00</td>
</tr>
<tr>
<td>Pholidocarpus</td>
<td>10.09 (1.19)</td>
<td>6</td>
<td>0.09 (0.65)</td>
</tr>
<tr>
<td>Physokentia</td>
<td>9.4</td>
<td>7</td>
<td>0.09</td>
</tr>
<tr>
<td>Psychococcus</td>
<td>8.7</td>
<td>2</td>
<td>0.03</td>
</tr>
<tr>
<td>Rhapis</td>
<td>7.7</td>
<td>11</td>
<td>0.14</td>
</tr>
<tr>
<td>Rhopalostylis</td>
<td>9.4</td>
<td>2</td>
<td>0.03</td>
</tr>
<tr>
<td>Satakentia</td>
<td>9.2</td>
<td>1</td>
<td>0.00</td>
</tr>
<tr>
<td>Serenoa</td>
<td>9.9 (8.96)</td>
<td>1</td>
<td>0.00 (0.00)</td>
</tr>
<tr>
<td>Solfa</td>
<td>5.5</td>
<td>1</td>
<td>0.00</td>
</tr>
<tr>
<td>Syagrus</td>
<td>8.5</td>
<td>59</td>
<td>0.21</td>
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<tr>
<td>Tahina</td>
<td>8.9</td>
<td>1</td>
<td>0.00</td>
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<td>Tectiphiala</td>
<td>4.8</td>
<td>1</td>
<td>0.00</td>
</tr>
<tr>
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<td>9.7</td>
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<td>0.05</td>
</tr>
<tr>
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Stem ages are derived from Baker and Couvreur (2013a, b) and crown ages from Bacon *et al.* (2013). X indicates unavailable data for the stem age.

Niche similarity statistics indicate that environmental niches among the four *Johannesteijsmannia* spp. are largely overlapping, even when the most conservative estimate of similarity is considered (Table 4). Together, the first two principal components of the six WorldClim variables explained 95.7% of the total variation in data. PC1 was primarily influenced by precipitation of the wettest quarter (loading 0.972), whereas PC2 primarily represented temperature seasonality (loading 0.725). In accordance with the niche similarity statistics, the climatic space inferred from the PCA shows a region occupied by all four species (Fig. 4), where *J. altifrons* occupies a wider niche space and the other species present narrower niche spaces with only slight differentiation between them.

Differences in elevation were not significantly different from each other based on an ANOVA ($P = 0.519$). There were gross similarities in mean

![Figure 4. Principal components analysis (PCoA) of ecological niche estimation. The first two PCA axes summarize 95.7% of the variation contained in the complete set of 19 WorldClim bioclimatic variables.](image-url)
elevation of *J. altifrons* and *J. lanceolata*, whereas both *J. magnifica* and *J. perakensis* were found at comparatively higher elevations.

**DISCUSSION**

We used multiple methods to assess species limits and genetic diversity as measured by morphological traits, genetic diversity, relationships and climatic niches among species. The genetic diversity among *Johannesteijsmannia* spp. is similar (Table 1) and *J. altifrons* had the highest genetic diversity, probably associated with its wide geographical range compared to its congeners. Furthermore, the genetic diversity of *Johannesteijsmannia* spp. is similar to that of other rain forest palms (e.g. Shapcott, 1998, 1999; Cardoso et al., 2000; de Lima et al., 2014). The maintenance of genetic diversity of all species is essential for their conservation. According to IUCN, all species in the genus are threatened or endangered (Johnson, 1996). Being obligate understorey plants, *Johannesteijsmannia* spp. do not survive when the forest canopy is removed (Look, 2007) and will probably be severely affected by deforestation due to ongoing forest conversion (Chan et al., 2012), e.g. for oil palm plantations in the region (Fitzherbert et al., 2008).

**Species and limited dispersal**

To assess species delimitations and whether gene flow occurs among currently recognized lineages, we gathered genetic and morphological evidence. Our Structure results showed that the individuals sampled form four clusters, implying there is little to no gene flow among species and PCoA of morphology detected no hybrid or intermediate individuals. Taken together, the four *Johannesteijsmannia* spp. are reproductively isolated and can be considered as independently evolving lineages, consistent with those recognized in the monograph (Dransfield, 1972).

A recent study in tropical species of *Psychotria L.* (Rubiaceae) found a significant positive relationship between species age and both realized range extent and range occupancy (Paul et al., 2009). With this, wide distributions are generally not achieved if little geological time has passed since the origin of a lineage, essentially trapping recently derived species in the same geographical space from which they originated. For this reason, distributions of *Johannesteijsmannia* spp. were predicted to have been established in recent geological times. The most recent phylogenetic analysis of Livistoninae corroborates this, with an estimated origin of current *Johannesteijsmannia* species diversity c. 4 Ma (Bacon et al., 2013). Although information on the natural history is lacking, applying one account of the mean generation time of understory palms (50 years; Ash, 1998) to *Johannesteijsmannia* suggests that c. 80 000 generations are sufficient to generate reproductive isolation among four lineages, but not enough to enable much dispersal out of the general area of diversification. Climate change since the late Pliocene (c. 2.5 Ma) may also have affected dispersal as a marked increase in montane and savanna vegetation accompanied a decline in tropical rain forest (Heaney, 1991), although to what extent remains unknown.

Although niche models show areas of suitable environments for all *Johannesteijsmannia* spp. in Java and Sumatra (Supporting Information, Fig. S1), only *J. altifrons* occurs outside Peninsular Malaysia. This is remarkable considering the derived phylogenetic position of *J. altifrons*, implying that in a short amount of time this species acquired one or more characteristics that enhanced dispersal capability or that the species is more ecologically tolerant, in contrast with the early divergent species that have restricted distributions. Potentially serving as an example of ecological release (Wilson, 1961; Roughgarden, 1972), *J. J. altifrons* expanded its ecological niche beyond that utilized by the other species with smaller range sizes. The mechanisms behind this process could be a broadening of its ecological requirements (e.g. populations in Borneo are confined to kerangas heath forests, whereas populations in Peninsular Malaysia are found in dipterocarp forests; Dransfield et al., 2008) combined with a change in its intrinsic dispersal ability by shifting the dispersal vector (e.g. Svenning, 2001), a hypothesis that remains to be tested.
Co-occurrence of species

Here, we consider co-occurrence to be defined as species found in the same geographical area that may experience some form of interaction, such as competitive exclusion or character displacement (Schluter, 2000). We predicted that Johannesteijsmannia lineages co-occur because gene flow causes incomplete reproductive isolation or because distinct species are maintained by some form of ecological divergence (Funk et al., 2006). We tested if co-occurrence of Johannesteijsmannia spp. is derived from niche segregation. Our results from niche modelling show that species are generally overlapping and, on the whole, not segregated based on climatic differences (Fig. 4, Table 4). One exception could be J. J. altifrons, which has a wider geographical range and hence is encountered across a wider niche breadth than its congeners (Fig. 4, Supporting Information, Fig. S1). A lack of environmental differentiation among species could also be due to the coarse resolution of the variables used, which may fail to detect possible differentiation at a finer scale (see Pearson & Dawson, 2003, for a review).

With a lack of definitive environmental divergence among reproductively isolated Johannesteijsmannia spp., we are left with the possibility that co-occurrence could be facilitated by other ecological factors, such as pollination biology. All Johannesteijsmannia spp. have a similar flower structure and size, but are highly distinct in inflorescence size and organization (Chan, Lim & Saw, 2011). Each Johannesteijsmannia sp. has a different floral odour, ranging widely from faintly sour to strongly fermented, which causes different pollinators to visit different species (Table 3 in Chan & Saw, 2011). Reinforcement of ecological divergence among sympatric congeners is detected in the temporal segregation of floral anthesis. For example, J. altifrons anthesis occurs between 5:00 and 10:00 a.m., whereas J. lanceolata peaks from 7:30 to 11:00 a.m., allowing for short periods of non-overlapping flower availability (Chan & Saw, 2011).

Floral traits and pollination syndrome can drive both microevolutionary (e.g. Harder & Johnson, 2009) and macroevolutionary (e.g. Barfod, Hagen & Borchsenius, 2011; Forest et al., 2014) patterns. Van der Niet et al. (2014) suggested that ecological speciation is the link between these two hierarchical levels of evolution and that adaptation and specialization derived from pollination-driven evolution are fundamental to plant diversification. Our results from a suite of data derived from densely sampled populations of Southeast Asian Johannesteijsmannia remain inconclusive, but ecological divergence may be caused by other factors than environmental niche differentiation, such as pollination biology. Niche segregation may require longer time scales for further dispersal opportunity, whereas the recent divergence times of Johannesteijsmannia spp. were sufficient to accumulate morphological differences.

Further studies are required that examine the mechanisms causing the formation of co-occurring distributions among closely related taxa in tropical forests, particularly in other plant lineages that can serve as direct comparisons to the results found here in Johannesteijsmannia. These studies will further identify general patterns in plant diversity and are fundamental to the conservation of species and populations. As widespread, keystone species with a long history in tropical rain forests (Couvreur, Forest & Baker, 2011), palms may be a particularly relevant study group, serving as representatives for Southeast Asian forests and perhaps tropical rain forests in general.

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**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Environmental niche models obtained from the Maxent analysis with georeferences also shown by black dots. Maps for each species show dark coloured areas where the model predicts high (> 0.8) habitat suitability (i.e. the probability of presence) and the lighter areas show habitat suitability between 0.5 and 0.8.

**Table S1.** Area under the curve (AUC), number of replicates (N) and variable importance of the Maxent species distribution model for each species.

**Table S2.** Response curves of each variable, by each model evaluated, for each species.
### Appendix 1.

List of *Johannesteijsmannia* localities in Southeast Asia. The number of samples (n) used in DNA analyses is shown for the localities surveyed for this study. Geographical data obtained elsewhere (Source) was used in conjunction with the samples to build environmental niche models for each species.

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Appendix 2.

Morphometric characters and their units of measurement for 203 accessions of *Johannesteijsmannia*. Characters measured and their units were STEM (discernible stem, present or absent), STEMHEI (discernible stem height, cm), STEMDIA (discernible stem diameter at widest, cm), LAMUND (lamina of the fifth leaf underside with white indumentum, present or absent), PLEATS (total number of pleats per lamina of the fifth leaf, number), LAMLEN (lamina length of the fifth leaf, cm), LAMWID (lamina width of the fifth leaf, cm), LAMWB (length of the widest part of lamina base of the fifth leaf, cm), PETLEN (petiole length, cm), PETWID (petiole width of the fifth leaf, cm) and PETDEP (petiole depth of the fifth leaf, cm).

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### Appendix 3.

Table of DNA sequences generated for this study with taxonomic authorities, sampled populations and GenBank accession numbers for the PRK and RPB2 genes.

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Cells containing the *symbol corresponds to samples without sequence data (i.e. unsuccessful PCRs). All samples with names greater than 0.1 are cloned sequences (see text), and therefore have no voucher specimen associated with them.