



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

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Four species are recognized in the understory palm genus *Johannesteijsmannia* (Arecaceae), 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 co-existence 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

ADDITIONAL KEYWORDS: Malesia – niche – Palmae – phylogenetics – speciation.

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

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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. (Arecaceae), 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 sympatry 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. (Arecaceae) 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, Malaysia (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 Malesian, 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)

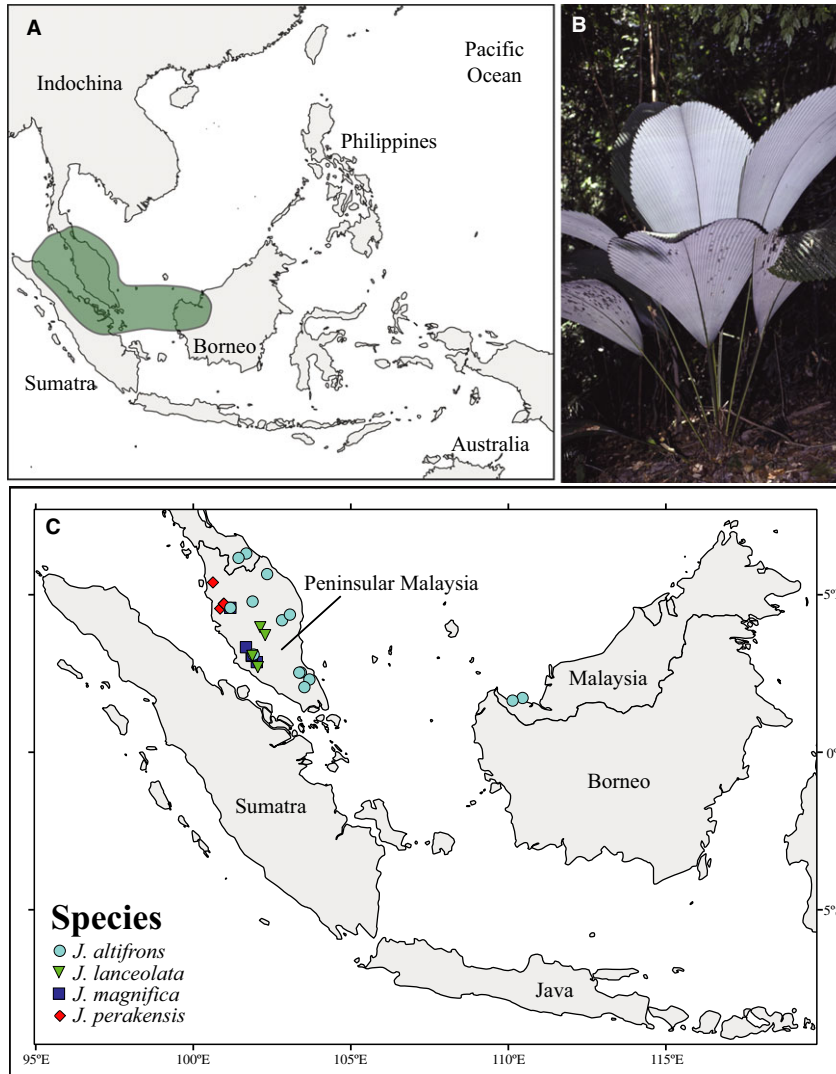


Figure 1. Map of Malesia (A) with the distribution of *Johannesteijsmannia* drawn in green, following Dransfield *et al.* (2008). (B) The beautiful leaves of *J. magnifica* are pictured in the upper left-hand corner (Photograph: John Dransfield). Sampling localities for all species (C).

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* Wurm 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 floras.

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 *MseI* (New England BioLabs) and ligated to double-stranded adaptors. Pre-selective and selective primers were based on adapter primer core sequences (*EcoRI* CTCGTAGACTGCGTACC and AATTGGTACGCAGTCTAC; *MseI* GACGATGAGTCCTGAG and TACTCAGGACTCAT) and selective primer combinations (*EcoRI*-AAG/*MseI*-CAC, *EcoRI*-ACA/*MseI*-CAG, *EcoRI*-ACT/*MseI*-CAT, *EcoRI*-AGC/*MseI*-CTG, *EcoRI*-AGG/*MseI*-CAA 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 ΔK statistical procedure (Evanno, Regnaut & Goudet, 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 Livistoninae (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 Broennimann *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 *ordiellipse* 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

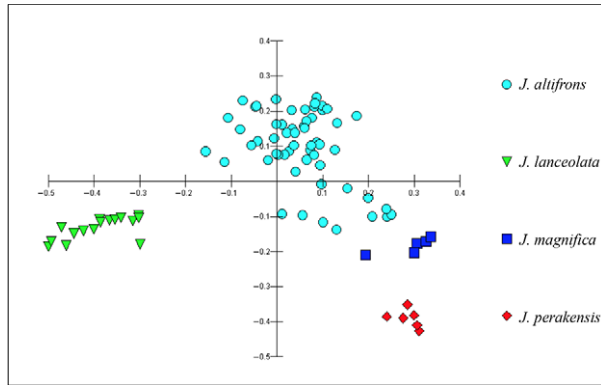


Figure 2. Species differentiation along the first and second principal coordinates when reproductive and vegetative characters were used. Four clear groupings were formed, corresponding to the four *Johannesteijsmannia* spp.

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 ($\geq 75\%$) 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

Table 1. Genetic diversity of *Johannesteijsmannia* OTUs

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

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

Table 2. Results from Structure analysis for co-dominant AFLP markers (Delta K; Evanno *et al.*, 2005) using Structure Harvester

<i>K</i>	Mean	Stdev	Ln'(K)	Ln''(K)	Delta K
	LnP(K)	LnP(K)			
1	-23999.93	8.87	NA	NA	NA
2	-21459.27	343.09	2540.67	364.27	1.06
3	-19282.87	976.65	2176.40	184.83	0.19
4	-17291.30	10.45	1991.57	1149.57	109.99
5	-16449.30	8.62	842.00	353.00	40.93
6	-15960.30	7.54	489.00	295.47	39.17
7	-15766.77	182.37	193.53	287.33	1.58
8	-15860.57	873.88	-93.80	41.03	0.05
9	-15995.40	512.78	-134.83	365.70	0.71
10	-15764.53	348.71	230.87	NA	NA

Bold font denotes the most likely results of four independent lineages in *Johannesteijsmannia*.

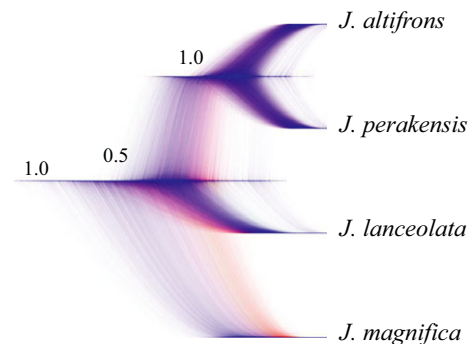


Figure 3. Coalescent species tree inferring the relationships among *Johannesteijsmannia* spp.; posterior probabilities are displayed above branches.

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*.

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

Genus	Stem (crown) node age	Number of species	Diversification rate [$\log(n)/t$]
<i>Acanthophoenix</i>	4.8	3	0.10
<i>Acoelorrhaphe</i>	9.9 (8.96)	1	0.00 (0.00)
<i>Actinokentia</i>	9.9	2	0.03
<i>Archontophoenix</i>	9.2	6	0.08
<i>Balaka</i>	5.5	12	0.20
<i>Brassiophoenix</i>	7.5	2	0.04
<i>Burretiokentia</i>	7.6	5	0.09
<i>Butia</i>	5.2	22	0.26
<i>Calyptrogyne</i>	8.3	17	0.15
<i>Calyptronomia</i>	8.3	3	0.06
<i>Carpentaria</i>	5.8	1	0.00
<i>Chambeyronia</i>	4.5	2	0.07
<i>Coccothrinax</i>	10	2	0.03
<i>Cyphosperma</i>	9.4	5	0.07
<i>Cyphophoenix</i>	7.6	4	0.08
<i>Drymophiloeus</i>	7.5	3	0.06
<i>Guihaia</i>	7.7	2	0.04
<i>Hedyscepe</i>	9.4	1	0.00
<i>Hemithrinax</i>	7.2	3	0.07
<i>Howea</i>	8.6	2	0.04
<i>Johannesteijsmannia</i>	10.09 (4.19)	4	0.06 (0.14)
<i>Jubaea</i>	5.2	1	0.00
<i>Kentiopsis</i>	4.4	4	0.14
<i>Kerriodoxa</i>	8.9	1	0.00
<i>Laccospadix</i>	8.6	1	0.00
<i>Lanonia</i>	X (8.63)	8	X (0.10)
<i>Leucothrinax</i>	7.2	1	0.00
<i>Lytocaryum</i>	8.54	4	0.07
<i>Normanbya</i>	8.1	1	0.00
<i>Pholidocarpus</i>	10.09 (1.19)	6	0.09 (0.65)
<i>Physokentia</i>	9.4	7	0.09
<i>Ptychococcus</i>	8.7	2	0.03
<i>Rhapis</i>	7.7	11	0.14
<i>Rhopalostylis</i>	9.4	2	0.03
<i>Satakentia</i>	9.2	1	0.00
<i>Serenoa</i>	9.9 (8.96)	1	0.00 (0.00)
<i>Solfia</i>	5.5	1	0.00
<i>Syagrus</i>	8.5	59	0.21
<i>Tahina</i>	8.9	1	0.00
<i>Tectiphiala</i>	4.8	1	0.00
<i>Thrinax</i>	9.7	3	0.05
<i>Veitchia</i>	9.1	11	0.11
<i>Wodyetia</i>	5.8	1	0.00

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 MODELS

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

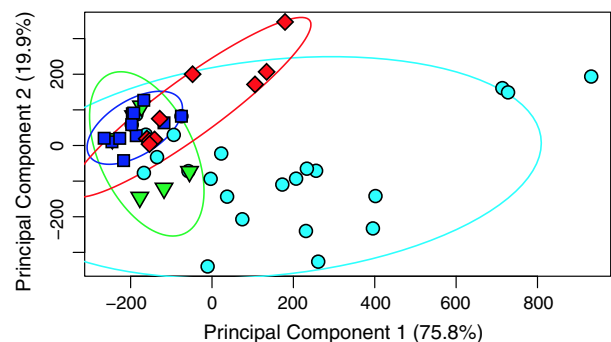


Figure 4. Principal components analysis (PCoA) of ecological niche estimation. The first two PCA axes summarize 95.7% of the variation contained in the complete set of 19 WorldClim bioclimatic variables.

Table 4. Niche similarity between *Johannesteijsmannia* spp. (maximum niche similarity) Above diagonal: Schoener's *D*; Below: Both statistics vary between 0 (completely dissimilar niches) and 1 diagonal: *I* statistic

Species	<i>J. altifrons</i>	<i>J. lanceolata</i>	<i>J. magnifica</i>	<i>J. perakensis</i>
<i>J. altifrons</i>	–	0.5008	0.4753	0.5914
<i>J. lanceolata</i>	0.7737	–	0.8122	0.6924
<i>J. magnifica</i>	0.7315	0.9613	–	0.6355
<i>J. perakensis</i>	0.8571	0.9179	0.8752	–

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 understorey 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. 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. Barford, 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 speciation 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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REFERENCES

- Ash J. 1998. Demography and production of *Balaka microcarpa* Burret (Arecaceae), a tropical understory palm in Fiji. *Australian Journal of Botany* **36**: 67–80.
- Bacon C. 2013. Biome evolution and biogeographical change through time. *Frontiers of Biogeography* **5**: 227–231.
- Bacon C, Bailey C. 2006. Taxonomy and conservation: a case study from *Chamaedorea alternans*. *Annals of Botany* **98**: 755–763.
- Bacon C, Baker WJ, Simmons MP. 2012. Miocene dispersal drives island radiations in the palms tribe Trachycarpeae (Arecaceae). *Systematic Biology* **61**: 426–442.
- Bacon C, Michonneau F, Henderson A, McKenna M, Milroy A, Simmons M. 2013. Geographic and taxonomic disparities in species diversity: dispersal and diversification rates across Wallace's Line. *Evolution* **67**: 2058–2071.

- Baker WJ, Couvreur TLP. 2013a.** Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. Historical biogeography. *Journal of Biogeography* **40**: 274–285.
- Baker WJ, Couvreur TLP. 2013b.** Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. II. Diversification history and origin of regional assemblages. *Journal of Biogeography* **40**: 286–298.
- Barfod AS, Hagen M, Borchsenius F. 2011.** Twenty-five years of progress in understanding pollination mechanisms in palms (Arecaceae). *Annals of Botany* **108**: 1503–1516.
- Bates H. 1863.** *A naturalist on the River Amazonas*. London: John Murray Press.
- Biomatters 2013.** Geneious version R6. Available at: <http://www.geneious.com>
- Blomberg SP, Garland TJ. 2002.** Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *Journal of Evolutionary Biology* **15**: 899–910.
- Borchsenius F. 2002.** Staggered flowering in four sympatric varieties of *Geonoma cuneata* (Palmae). *Biotropica* **34**: 603–606.
- Borchsenius F, Lozada T, Knudsen JT. 2016.** Reproductive isolation of sympatric forms of the understory palm *Geonoma macrostachys* in western Amazonia. *Botanical Journal of the Linnean Society* doi:10.1111/boj.12428.
- Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier LC, Yoccoz NG, Thuiller W, Fortin M-J, Randin C, Zimmermann NE, Graham CH, Guisan A. 2012.** Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography* **21**: 481–497.
- Cardoso S, Eloy N, Provan J, Cardoso M, Ferreira P. 2000.** Genetic differentiation of *Euterpe edulis* Mart. populations estimated by AFLP analysis. *Molecular Ecology* **9**: 1753–1760.
- Chan Y, Lim A, Saw L. 2011.** Reproductive biology of the endangered and endemic palm *Johannesteijsmannia lanceolata* (Arecaceae). *Journal of Tropical Forest Science* **23**: 213–221.
- Chan Y, Saw L. 2011.** Notes on the pollination ecology of the palm genus *Johannesteijsmannia* (Arecaceae). *Journal of Pollination Ecology* **6**: 108–117.
- Chan YM, Chua LSL, Saw LG. 2012.** Towards the conservation of Malaysian *Johannesteijsmannia* (Palmae). *Garden's Bulletin, Singapore* **63**: 425–432.
- Couvreur TLP, Baker WJ. 2013.** Tropical rain forest evolution: palms as a model group. *BMC Biology* **11**: e48.
- Couvreur TLP, Forest F, Baker WJ. 2011.** Origin and global diversification patterns of tropical rain forests: inferences from a complete genus-level phylogeny of palms. *BMC Biology* **9**: 44.
- Coyne J, Orr H. 2004.** *Speciation*. Sunderland: Sinauer Associates.
- Darwin C. 1859.** *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray.
- Dawson I, Simon A, Waugh R, Powell W. 1995.** Diversity and genetic differentiation among subpopulations of *Gliricidia sepium* revealed by PCR-based assays. *Heredity* **75**: 10–18.
- Dietrich B, Wehner R. 2003.** Sympatry and allopatry in two desert ant sister species: how do *Cataglyphis bicolor* and *C. savignyi* coexist? *Oecologia* **136**: 63–72.
- Dransfield J. 1972.** The genus *Johannesteijsmannia* H.E. Moore Jr. *Garden's Bulletin, Singapore* **26**: 63–83.
- Dransfield J. 1987.** Bicentric distributions in Malesia as exemplified by palms. In: Whitmore T, ed. *Biogeographical evolution of the Malay Archipelago*. Oxford: Clarendon Press, 60–72.
- Dransfield J, Uhl N, Asmussen C, Baker WJ, Harley M, Lewis C. 2008.** *Genera palmarum: the evolution and classification of palms*. Kew: Kew Publishing.
- Earl D, Vonholdt B. 2012.** STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources* **4**: 359–361.
- Edgar R. 2004.** MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* **32**: 1792–1797.
- Elith J, Graham C, Anderson R, Dudík M, Ferrier S, Guisan A, Hijmans R, Huettmann F, Leathwick J, Lehmann A, Li J, Lohmann L, Loiselle B, Manion G, Moritz C, Nakamura M, Nakazawa Y, McC Overton J, Peterson A, Phillips S, Richardson K, Scachetti-Pereira R, Schapire R, Soberón J, Williams S, Wisz M, Zimmermann N. 2006.** Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**: 129–151.
- Esselstyn J, Timm R, Brown R. 2009.** Do geological or climatic processes drive speciation in dynamic archipelagos? The tempo and mode of diversification in Southeast Asian shrews. *Evolution* **63**: 2595–2610.
- Evanno G, Regnaut S, Goudet J. 2005.** Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular Ecology* **14**: 2611–2620.
- Excoffier L, Smouse P, Quattro J. 1992.** Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics* **131**: 479–491.
- Fitzherbert EB, Struebig MJ, Morel A, Danielsen F, Bruhl C, Donald PF, Phalan B. 2008.** How will oil palm expansion affect biodiversity? *Trends in Ecology and Evolution* **23**: 538–545.
- Forest F, Goldblatt P, Manning JC, Baker D, Colville JF, Devey DS, Jose S, Kaye M, Muerki S. 2014.** Pollinator shifts as triggers of speciation in painted petal irises (*Lapeirousia*: Iridaceae). *Annals of Botany* **113**: 357–371.
- Funk DJ, Nosil P, Etges WJ. 2006.** Ecological divergence exhibits consistently positive associations with reproductive isolation across disparate taxa. *Proceedings of the National Academy of Sciences, USA* **103**: 3209–3213.
- Gower DJ, Johnson KG, Richardson JE, Rosen BR, Ruber L, Williams ST. 2012.** *Biotic evolution and environmental change in Southeast Asia*. Cambridge: Cambridge University Press.
- Gower JC. 1971.** A general coefficient of similarity and some of its properties. *Biometrics* **27**: 857–871.

- Hall R. 2009.** Southeast Asia's changing palaeogeography. *Blumea* **54**: 148–161.
- Harder LD, Johnson SD. 2009.** Darwin's beautiful contrivances: evolutionary and functional evidence for floral adaptation. *New Phytologist* **183**: 530–545.
- Heaney LR. 1991.** A synopsis of climatic and vegetational change in Southeast Asia. *Climate Change* **19**: 53–61.
- Heled J, Drummond A. 2010.** Bayesian inference of species trees from multilocus data. *Molecular Biology and Evolution* **27**: 570–580.
- Heled J, Drummond AJ. 2012.** Calibrated tree priors for relaxed phylogenetics and divergence time estimation. *Systematic Biology* **61**: 138–149.
- Henderson A. 2002.** Phenetic and phylogenetic analysis of *Reinhardtia* (Palmae). *American Journal of Botany* **89**: 1491–1502.
- Henderson A. 2004.** A multivariate analysis of *Hyospathe* (Palmae). *American Journal of Botany* **91**: 953–965.
- Henderson A. 2006.** Traditional morphometrics in plant systematics and its role in palm systematics. *Botanical Journal of the Linnean Society* **151**: 103–111.
- Henderson A, Ferreira E. 2002.** A morphometric study of *Synechanthus* (Palmae). *Systematic Botany* **27**: 693–702.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005.** Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**: 1965–1978.
- Huey RB, Pianka ER. 1977.** Patterns of niche overlap among broadly sympatric versus narrowly sympatric Kalahari lizards (Scinidae: *Mabuya*). *Ecology* **58**: 119–128.
- Johnson D. 1996.** *Palms: their conservation and sustained utilization*. Status survey and conservation action plan. Gland: IUCN.
- Johnson SD. 2006.** Pollinator-driven speciation in plants. In: Harder LD, Barrett SCH, eds. *The ecology and evolution of flowers*. Oxford: Oxford University Press, 295–310.
- Knudsen JT. 1999.** Floral scent differentiation among coflowering, sympatric species of *Geonoma* (Arecaceae). *Plant Species Biology* **14**: 137–142.
- Knudsen JT. 2002.** Variation in floral scent composition within and between populations of *Geonoma macrostachys* (Arecaceae) in the western Amazon. *American Journal of Botany* **89**: 1772–1778.
- Legendre L, Legendre P. 1983.** *Numerical ecology*. New York: Elsevier Scientific.
- Lewis C, Doyle J. 2002.** A phylogenetic analysis of tribe Areceae (Arecaceae) using two low-copy nuclear genes. *Plant Systematics and Evolution* **236**: 1–17.
- Ley AC, Hardy OJ. 2014.** Contrasting patterns of gene flow between sister plant species in the understorey of African moist forests – the case of sympatric and parapatric Marantaceae species. *Molecular Phylogenetics and Evolution* **77**: 264–274.
- de Lima NE, Lima-Ribeiro MS, Faleiro Tinoco C, Carina Terribile L, Collevatti RG. 2014.** Phylogeographic and ecological niche modeling, coupled with the fossil pollen record, unravel the demographic history of a Neotropical swamp through the Quaternary. *Journal of Biogeography* **41**: 673–686.
- Lobo JM, Jiménez-Valverde A, Real R. 2008.** AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* **17**: 145–151.
- Loo A, Tan H, Kumar P, Saw L. 2001.** Intraspecific variation in *Licuala glabra* Griff. (Palmae) in Peninsular Malaysia – a morphometric analysis. *Biological Journal of the Linnean Society* **72**: 115–128.
- Look S. 2007.** *Population genetics and phylogeny of the Malaysian palm genus Johannesteijsmannia H.E.Moore (Palmae)*. PhD thesis, Biological Sciences, The National University of Singapore.
- Losos JB. 2008.** Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters* **11**: 995–1007.
- MacArthur RH. 1972.** *Geographical ecology*. New York: Harper Row.
- Magallón S, Sanderson MJ. 2001.** Absolute diversification rates in angiosperm clades. *Evolution* **55**: 1762–1780.
- Morley R. 2000.** *Origin and evolution of tropical rain forests*. New York: John Wiley & Sons.
- Murray M, Thompson W. 1980.** Rapid isolation of high molecular weight plant DNA. *Nucleic Acids Research* **8**: 4321–4325.
- Myers N, Mittermeier R, Mittermeier C, da Fonseca G, Kent J. 2000.** Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858.
- Okanasan J, Guillaume Blanchet F, Kindt R, Legendre P, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H. 2011.** vegan: community ecology package. *R package version 1*: 17–10.
- Palmweb. 2016.** Palms of the World online. Available at: <http://palmweb.org> Accessed 2014.
- Papadopoulos AST, Kaye M, Devaux C, Hipperson H, Lighten J, Dunning LT, Hutton I, Baker WJ, Butlin RK, Savolainen V. 2014.** Evaluation of genetic isolation within an island flora reveals unusually widespread local adaptation and supports sympatric speciation. *Philosophical Transactions of the Royal Society of London: Series B* **369**: e20130342.
- Paul JR, Morton C, Taylor CM, Tonsor SJ. 2009.** Evolutionary time for dispersal limits the extant but not the occupancy of species' potential ranges in the tropical plant genus *Psychotria* (Rubiaceae). *The American Naturalist* **173**: 188–199.
- Pearson RG, Dawson TP. 2003.** Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* **12**: 361–371.
- Phillips SJ, Dudik M, Schapire RE. 2004.** A maximum entropy approach to species distribution modeling. In: *Proc. of the 21st International Conference on Machine Learning*, Banff, Canada, 2004.
- Pritchard J, Stephens M, Donnelly P. 2000.** Inference of population structure using multilocus genotype data. *Genetics* **155**: 945–959.
- R Development Team. 2008.** A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

- Rambaut A, Drummond AJ. 2007.** Tracer v1.4. Available from <http://beast.bio.ed.ac.uk/software/tracer/>
- Restrepo Correa Z, Nunez Avellaneda LA, Gonzalez-Caro S, Velasquez-Puentes F, Bacon CD. 2016.** Exploring palm – pollinator interaction across geographic and environmental gradients. *Botanical Journal of the Linnean Society* doi:10.1111/boj.12443.
- Roncal J. 2006.** Habitat differentiation of sympatric *Geonoma macrostachys* (Arecaceae) varieties in Peruvian lowland forests. *Journal of Tropical Ecology* **22**: 483–486.
- Roncal J, Francisco-Ortega J, Asmussen C, Lewis C. 2005.** Molecular phylogenetic of tribe Geonomeae (Arecaceae) using nuclear DNA sequence of phosphoribulokinase and RNA polymerase II. *Systematic Botany* **30**: 275–283.
- Roughgarden J. 1972.** Evolution of niche width. *American Naturalist* **106**: 683–718.
- Savolainen V, Anstett M-C, Lexer C, Hutton I, Clarkson JJ, Norup MV, Powell WP, Springate D, Salamin N, Baker WJ. 2006.** Sympatric speciation in palms on an oceanic island. *Nature* **441**: 210–213.
- Schluter D. 2000.** *The ecology of adaptive radiation*. Oxford: Oxford University Press.
- Schluter D, Conte GL. 2009.** Genetics and ecological speciation. *Proceedings of the National Academy of Sciences, USA* **106**: 9955–9962.
- Schneider S, Roessli D, Excoffier L. 2000.** Arlequin ver. 2.000: a software for population genetics data analysis. Genetics and Biometry Laboratory, University of Geneva, Switzerland.
- Shapcott A. 1998.** The patterns of genetic diversity in *Carpentaria acuminata* (Arecaceae), and rainforest history in northern Australia. *Molecular Ecology* **7**: 833–847.
- Shapcott A. 1999.** Comparison of the population genetics and densities of five *Pinanga* palm species at Kuala Belalong, Brunei. *Molecular Ecology* **8**: 1641–1654.
- Simpson GG. 1944.** *Tempo and mode in evolution*. New York: Columbia University Press.
- Svenning JC. 2001.** On the role of microenvironmental heterogeneity in the ecology and diversification of Neotropical rain-forest palms (Arecaceae). *Botanical Review* **67**: 1–53.
- Van der Niet T, Peakall R, Johnson SD. 2014.** Pollinator-driven ecological speciation in plants: new evidence and future perspectives. *Annals of Botany* **113**: 199–211.
- Vos P, Hogers R, Bleeker M, Rijans M, van de Lee T, Hornes M, Fritjers A, Plot J, Peleman J, Kuiper M, Zabeau M. 1995.** AFLP: a new technique for DNA fingerprinting. *Nucleic Acids Research* **23**: 311–321.
- Wallace A. 1865.** On the phenomena of variation and geographical distributions as illustrated by the Papilionidæ of the Malayan region. *Transactions of the Linnean Society of London* **25**: 1–71.
- Wilson EO. 1961.** The nature of the taxon cycle in the Melanesian ant fauna. *American Naturalist* **95**: 169–193.
- Wright S. 1965.** The interpretation of genetic structure by F-statistics with species regard to systems of mating. *Evolution* **19**: 355–430.
- Yeh F, Yang R, Boyle T. 1999.** POPGENE version 1.31. <http://www.ualberta.ca/~fyeh/popgene.html>

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.

Species	Country	Locality	n	Latitude	Longitude	Source
<i>Johannesteijsmannia altifrons</i>	Malaysia	Johor	6	2.06628	103.52614	This study
<i>Johannesteijsmannia altifrons</i>	Malaysia	Johor	13	2.30978	103.68522	This study
<i>Johannesteijsmannia altifrons</i>	Malaysia	Johor	8	2.53117	103.41411	This study
<i>Johannesteijsmannia altifrons</i>	Malaysia	Johor	8	2.52719	103.36375	This study
<i>Johannesteijsmannia altifrons</i>	Malaysia	Kelantan	8	4.78428	101.88136	This study
<i>Johannesteijsmannia altifrons</i>	Malaysia	Kelantan	8	5.65506	102.34322	This study
<i>Johannesteijsmannia altifrons</i>	Malaysia	Pahang	8	4.18939	102.81589	This study
<i>Johannesteijsmannia altifrons</i>	Malaysia	Perak	8	4.58331	101.17739	This study
<i>Johannesteijsmannia altifrons</i>	Malaysia	Sarawak	8	1.63897	110.13547	This study
<i>Johannesteijsmannia altifrons</i>	Malaysia	Sarawak	8	1.72292	110.45144	This study
<i>Johannesteijsmannia altifrons</i>	Malaysia	Selangor	8	3.10044	101.91469	This study
<i>Johannesteijsmannia altifrons</i>	Malaysia	Terengganu	8	4.36811	103.06669	This study
<i>Johannesteijsmannia altifrons</i>	Thailand	Narathiwat	9	6.16844	101.43631	This study
<i>Johannesteijsmannia altifrons</i>	Thailand	Narathiwat	8	6.30839	101.68183	This study
<i>Johannesteijsmannia altifrons</i>	Indonesia	Aceh	–	4.33333	97.91667	Royal Botanic Gardens, Kew, Herbarium
<i>Johannesteijsmannia altifrons</i>	Indonesia	North Sumatra	–	4.03333	98.20000	Royal Botanic Gardens, Kew, Herbarium
<i>Johannesteijsmannia altifrons</i>	Indonesia	Jambi	–	-0.93333	102.50000	Royal Botanic Gardens, Kew, Herbarium
<i>Johannesteijsmannia altifrons</i>	Thailand	Yala	–	5.75000	101.25000	Royal Botanic Gardens, Kew, Herbarium
<i>Johannesteijsmannia altifrons</i>	Thailand	Yala	–	5.83333	101.30000	Royal Botanic Gardens, Kew, Herbarium
<i>Johannesteijsmannia altifrons</i>	Thailand	Narathiwat	–	6.00000	101.83300	GBIF (http://www.gbif.org/species/2731747)
<i>Johannesteijsmannia altifrons</i>	Thailand	Songkhla	–	7.02100	100.29100	GBIF (http://www.gbif.org/species/2731747)
<i>Johannesteijsmannia altifrons</i>	Malaysia	Pahang	–	4.56667	102.43333	Royal Botanic Gardens, Kew, Herbarium
<i>Johannesteijsmannia altifrons</i>	Malaysia	Selangor	–	3.05000	101.90000	Royal Botanic Gardens, Kew, Herbarium
<i>Johannesteijsmannia altifrons</i>	Malaysia	Sarawak	–	1.71667	110.44722	Royal Botanic Gardens, Kew, Herbarium
<i>Johannesteijsmannia lanceolata</i>	Malaysia	Negeri Sembilan	8	1.96097	99.30178	This study

Appendix 1. *Continued*

Species	Country	Locality	<i>n</i>	Latitude	Longitude	Source
<i>Johannesteijsmannia lanceolata</i>	Malaysia	Pahang	8	3.71694	102.28111	This study
<i>Johannesteijsmannia lanceolata</i>	Malaysia	Pahang	8	3.96739	102.12467	This study
<i>Johannesteijsmannia lanceolata</i>	Malaysia	Selangor	9	3.05808	101.87289	This study
<i>Johannesteijsmannia lanceolata</i>	Malaysia	Pahang	–	3.72519	102.11542	Dransfield (1972)
<i>Johannesteijsmannia lanceolata</i>	Malaysia	Selangor	–	3.11286	101.82403	Dransfield (1972)
<i>Johannesteijsmannia magnifica</i>	Malaysia	Negeri Sembilan	8	2.86047	102.01667	This study
<i>Johannesteijsmannia magnifica</i>	Malaysia	Perak	8	4.58331	101.17733	This study
<i>Johannesteijsmannia magnifica</i>	Malaysia	Selangor	8	3.05742	101.85450	This study
<i>Johannesteijsmannia magnifica</i>	Malaysia	Selangor	8	3.08178	101.86294	This study
<i>Johannesteijsmannia magnifica</i>	Malaysia	Selangor	8	3.33342	101.67228	This study
<i>Johannesteijsmannia magnifica</i>	Malaysia	Negeri Sembilan	–	2.82814	102.08647	Dransfield (1972)
<i>Johannesteijsmannia magnifica</i>	Malaysia	Negeri Sembilan	–	2.85778	101.99133	Dransfield (1972)
<i>Johannesteijsmannia magnifica</i>	Malaysia	Negeri Sembilan	–	2.92903	101.97939	Dransfield (1972)
<i>Johannesteijsmannia magnifica</i>	Malaysia	Selangor	–	3.01175	101.79431	Dransfield (1972)
<i>Johannesteijsmannia magnifica</i>	Malaysia	Selangor	–	3.13061	101.75244	Dransfield (1972)
<i>Johannesteijsmannia magnifica</i>	Malaysia	Selangor	–	3.05000	101.90000	Royal Botanic Gardens, Kew, Herbarium
<i>Johannesteijsmannia perakensis</i>	Malaysia	Kedah	8	5.39039	100.62394	This study
<i>Johannesteijsmannia perakensis</i>	Malaysia	Perak	8	4.56072	100.85214	This study
<i>Johannesteijsmannia perakensis</i>	Malaysia	Perak	8	4.71589	100.96675	This study
<i>Johannesteijsmannia perakensis</i>	Malaysia	Perak	8	4.71364	100.97197	This study
<i>Johannesteijsmannia perakensis</i>	Malaysia	Perak	–	4.55856	100.90103	Dransfield (1972)
<i>Johannesteijsmannia perakensis</i>	Malaysia	Perak	–	4.62458	100.92469	Dransfield (1972)
<i>Johannesteijsmannia perakensis</i>	Malaysia	Perak	–	4.69697	100.89992	Dransfield (1972)
<i>Johannesteijsmannia perakensis</i>	Malaysia	Perak	–	4.75164	100.91103	Dransfield (1972)
<i>Johannesteijsmannia perakensis</i>	Malaysia	Perak	–	4.63847	100.78414	Dransfield (1972)
<i>Johannesteijsmannia perakensis</i>	Malaysia	Perak	–	5.16667	100.95000	Royal Botanic Gardens, Kew, Herbarium

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), STEMEDIA (discernible stem *J* 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 width of the fifth leaf, cm), PETWID (petiole depth of the fifth leaf, cm).

Individual	STEM	STEMHEI	STEMEDIA	LAMUND	PLEATS	LAMLEN	LAMWID	LAMWB	PETLEN	PETWID	PETDEP
A1	0	0	0	0	58	203.0	70.5	108.0	75.5	2.1	1.7
A2	0	0	0	0	57	214.5	78.5	116.5	108.0	2.4	1.7
A3	0	0	0	0	53	244.4	66.3	132.0	150.5	2.1	1.6
A4	0	0	0	0	59	218.5	92.0	79.5	100.5	2.1	1.5
A5	0	0	0	0	57	231.2	72.4	113.8	117.0	2.0	1.6
A6	0	0	0	0	64	241.2	100.4	133.0	80.0	2.4	2.0
A7	0	0	0	0	64	214.8	113.4	120.6	68.0	2.5	1.6
A8	0	0	0	0	63	231.8	96.7	120.3	127.5	2.2	1.4
A9	0	0	0	0	57	234.5	96.0	105.5	148.5	2.1	1.5
A10	0	0	0	0	58	250.5	63.2	110.0	164.5	1.8	1.3
A11	0	0	0	0	53	259.5	87.2	121.8	144.3	1.9	1.8
A12	0	0	0	0	59	215.9	79.0	125.0	127.0	1.8	1.5
A13	0	0	0	0	50	208.0	56.8	110.0	131.8	1.5	1.3
A14	0	0	0	0	53	245.6	72.2	140.8	143.5	1.8	1.3
A15	0	0	0	0	59	270.5	74.0	136.5	220.1	2.0	1.9
A16	0	0	0	0	58	240.9	68.8	99.4	247.5	2.7	1.8
A17	0	0	0	0	59	239.6	76.6	107.4	188.5	2.2	1.7
A18	0	0	0	0	65	204.0	93.0	122.0	232.0	2.0	1.5
A19	0	0	0	0	65	193.0	129.0	101.0	176.0	2.5	2.0
A20	0	0	0	0	56	207.0	75.0	95.0	168.0	2.1	1.3
A21	0	0	0	0	64	246.0	104.0	124.0	165.0	2.6	2.0
A22	0	0	0	0	59	232.0	84.0	106.0	118.0	2.3	1.7
A23	0	0	0	0	62	224.0	105.0	94.0	205.5	2.6	1.8
A24	0	0	0	0	56	217.0	85.0	90.0	210.0	2.2	1.7
A25	0	0	0	0	62	216.0	101.0	109.0	221.0	2.5	2.1
A26	0	0	0	0	65	248.0	116.0	121.0	210.0	2.7	3.0
A27	0	0	0	0	63	210.0	100.0	97.0	199.0	2.2	1.7
A28	0	0	0	0	64	251.0	94.0	113.0	192.0	2.3	1.8
A29	0	0	0	0	60	244.0	100.0	144.0	207.0	2.1	1.9
A30	0	0	0	0	74	251.0	124.0	129.0	123.0	2.7	1.7
A31	0	0	0	0	74	186.0	97.0	103.0	126.0	2.4	1.5
A32	0	0	0	0	65	249.0	115.0	135.0	221.0	2.5	2.4
A33	0	0	0	0	73	221.0	115.0	129.0	159.0	2.6	2.2

Appendix 2. *Continued*

Individual	STEM	STEMHEI	STEMDIA	LAMUND	PLEATS	LAMLEN	LAMWID	LAMWB	PETLEN	PETWID	PETDEP
A34	0	0	0	0	67	236.0	107.0	104.0	106.0	2.4	1.8
A35	0	0	0	0	63	256.0	96.0	104.5	121.0	3.0	2.2
A36	0	0	0	0	58	237.5	100.0	110.0	172.0	2.5	2.3
A37	0	0	0	0	65	229.0	110.0	115.0	117.0	2.5	1.6
A38	0	0	0	0	61	269.0	113.0	146.0	213.0	2.6	2.4
A39	0	0	0	0	59	277.0	98.0	111.0	151.0	2.7	1.6
A40	0	0	0	0	66	268.0	94.0	140.0	148.0	2.5	2.3
A41	0	0	0	0	60	261.0	112.0	105.0	205.0	3.2	3.0
A42	0	0	0	0	60	280.0	113.0	112.0	164.0	3.0	2.9
A43	0	0	0	0	66	288.0	93.0	162.0	126.0	2.6	2.5
A44	0	0	0	0	54	290.0	75.0	151.0	163.0	2.5	2.0
A45	0	0	0	0	52	278.0	72.0	135.0	155.0	2.3	2.2
A46	0	0	0	0	44	266.0	59.0	132.0	68.0	2.0	1.8
A47	0	0	0	0	47	269.0	64.0	136.0	98.0	2.0	2.0
A48	0	0	0	0	52	231.5	51.5	91.0	61.5	2.5	2.2
A49	0	0	0	0	50	231.5	69.0	129.0	66.0	2.5	2.3
A50	0	0	0	0	49	280.0	64.0	143.0	141.0	2.0	2.0
A51	0	0	0	0	43	229.0	97.0	96.0	102.0	1.8	1.6
A52	0	0	0	0	49	320.0	68.0	158.0	147.0	2.5	2.7
A53	0	0	0	0	39	283.5	56.0	127.0	107.0	2.5	1.4
A54	0	0	0	0	42	224.0	58.0	123.0	104.0	2.5	2.0
A55	0	0	0	0	44	237.0	58.0	142.0	129.5	2.5	1.5
A56	0	0	0	0	49	221.0	70.5	122.0	146.0	2.5	2.0
A57	0	0	0	0	52	234.5	77.0	132.0	165.5	2.5	2.0
A58	0	0	0	0	53	282.0	78.0	139.0	157.0	2.7	2.6
A59	0	0	0	0	54	241.0	71.0	140.0	140.5	2.4	2.5
A60	0	0	0	0	46	281.0	73.0	159.0	120.0	2.4	2.5
A61	0	0	0	0	49	263.0	71.0	137.0	92.5	2.3	2.0
A62	0	0	0	0	48	275.0	77.5	136.0	98.0	2.6	2.5
A63	0	0	0	0	49	325.0	85.0	143.0	152.0	2.5	2.6
A64	0	0	0	0	52	233.5	120.5	110.0	199.0	3.0	2.5
A65	0	0	0	0	63	272.0	102.0	116.0	221.0	2.7	2.3
A66	0	0	0	0	56	274.0	85.0	151.0	203.0	2.4	2.2
A67	0	0	0	0	66	291.0	108.0	164.0	242.5	2.9	2.5
A68	0	0	0	0	62	221.0	96.0	125.0	132.0	2.1	1.7
A69	0	0	0	0	63	253.0	99.0	142.0	152.0	2.4	1.8
A70	0	0	0	0	58	251.0	90.0	116.0	204.0	2.0	1.7
A71	0	0	0	0	61	259.0	88.0	132.0	174.0	2.4	1.9
A72	0	0	0	0	59	210.0	85.5	122.0	232.0	2.4	2.1

Appendix 2. Continued

Individual	STEM	STEMHEI	STEMDIA	LAMUND	PLEATS	LAMLEN	LAMWID	LAMWB	PETLEN	PETWID	PETDEP
A73	0	0	0	0	52	228.5	100.0	109.5	194.0	2.5	2.3
A74	0	0	0	0	50	238.5	93.0	113.0	92.5	2.5	2.0
A75	0	0	0	0	59	254.1	79.0	144.5	186.0	2.6	2.0
A76	0	0	0	0	56	177.5	96.0	91.0	117.0	2.1	1.8
A77	0	0	0	0	54	247.0	92.0	113.0	232.5	2.5	2.0
A78	0	0	0	0	55	250.5	80.0	120.5	246.5	2.5	2.2
A79	0	0	0	0	56	251.0	89.0	120.0	173.5	2.6	2.2
A80	0	0	0	0	53	238.5	100.0	120.0	129.0	2.5	2.0
A81	0	0	0	0	59	187.5	95.0	91.0	207.0	2.5	2.2
A82	0	0	0	0	55	222.0	78.0	120.0	167.5	2.2	2.1
A83	0	0	0	0	53	210.0	80.0	103.5	130.0	2.1	1.8
A84	0	0	0	0	54	197.5	90.0	98.0	181.0	2.4	2.2
A85	0	0	0	0	61	199.0	103.0	96.0	145.7	2.4	2.0
A86	0	0	0	0	63	244.5	106.0	122.0	181.0	2.9	2.3
A87	0	0	0	0	70	240.0	110.0	125.0	230.0	2.5	2.3
A88	0	0	0	0	59	241.5	83.5	140.0	183.5	2.0	1.8
A89	0	0	0	0	63	165.0	84.5	82.0	124.0	1.8	1.5
A90	0	0	0	0	62	160.0	89.0	70.0	127.0	2.0	1.6
A91	0	0	0	0	57	180.0	79.0	83.0	136.0	2.1	1.9
A92	0	0	0	0	60	175.5	73.5	93.0	122.0	1.7	1.5
A93	0	0	0	0	63	217.2	93.0	89.0	167.0	2.1	1.9
A94	0	0	0	0	54	189.0	93.0	76.0	194.0	2.4	1.9
A95	0	0	0	0	52	221.8	84.0	108.0	117.5	2.5	2.0
A96	0	0	0	0	56	170.0	87.0	84.0	160.0	2.0	1.5
A97	0	0	0	0	59	180.0	87.0	88.0	137.0	1.9	1.4
A98	0	0	0	0	59	267.0	105.5	133.0	215.0	3.2	2.8
A99	0	0	0	0	49	214.6	79.0	95.0	149.0	2.1	1.8
A100	0	0	0	0	54	186.0	84.0	100.5	181.5	2.5	1.8
A101	0	0	0	0	61	224.5	105.0	123.0	177.0	2.5	2.2
A102	0	0	0	0	58	197.0	94.0	100.0	146.5	2.0	1.9
A103	0	0	0	0	65	243.0	95.0	128.0	243.0	2.4	1.9
A104	0	0	0	0	55	238.0	105.0	112.0	178.0	2.5	2.3
A105	0	0	0	0	50	186.0	70.0	95.0	133.0	1.8	1.6
L1	0	0	0	0	41	223.0	45.0	124.0	157.0	2.0	1.7
L2	0	0	0	0	43	215.0	43.0	126.0	144.5	1.9	1.8
L3	0	0	0	0	40	248.0	48.0	140.0	120.0	2.1	1.5
L4	0	0	0	0	52	228.0	61.0	119.0	126.0	2.2	2.0
L5	0	0	0	0	45	195.0	53.0	89.0	104.0	1.7	1.8
L6	0	0	0	0	44	241.5	40.0	94.0	139.0	1.9	1.6

Appendix 2. *Continued*

Individual	STEM	STEMHEI	STEMDIA	LAMUND	PLEATS	LAMLEN	LAMWID	LAMWB	PETLEN	PETWID	PETDEP
L7	0	0	0	0	44	190.0	51.0	108.0	133.0	1.7	1.3
L8	0	0	0	0	42	173.0	39.0	96.0	136.0	1.6	1.3
L9	0	0	0	0	44	242.5	34.5	102.0	105.0	1.7	1.4
L10	0	0	0	0	45	211.5	41.5	79.5	64.0	2.0	1.5
L11	0	0	0	0	43	217.0	31.5	95.0	27.5	1.7	1.2
L12	0	0	0	0	41	223.5	45.5	81.0	73.5	1.8	1.5
L13	0	0	0	0	45	240.0	46.0	111.5	121.0	1.8	2.0
L14	0	0	0	0	46	222.0	36.5	112.0	159.0	2.0	1.5
L15	0	0	0	0	38	215.0	40.0	80.5	71.0	1.7	1.0
L16	0	0	0	0	44	253.0	45.0	116.0	192.0	1.4	2.2
L17	0	0	0	0	47	294.0	34.5	142.0	138.5	2.5	2.0
L18	0	0	0	0	35	218.0	26.0	68.0	135.9	1.5	1.3
L19	0	0	0	0	44	225.5	35.0	106.0	161.0	1.8	1.7
L20	0	0	0	0	40	210.0	27.0	104.0	118.0	1.3	1.4
L21	0	0	0	0	40	280.0	32.5	115.0	115.0	2.2	2.3
L22	0	0	0	0	35	253.0	25.0	122.5	142.0	1.3	1.3
L23	0	0	0	0	36	212.0	28.0	83.5	89.0	1.3	1.2
L24	0	0	0	0	39	299.0	26.5	126.0	137.0	1.8	1.6
L25	0	0	0	0	42	257.5	35.0	122.0	135.0	1.8	1.7
M1	0	0	0	1	61	220.0	123.0	115.0	180.0	2.6	1.9
M2	0	0	0	1	61	219.0	99.0	107.0	233.0	2.3	2.0
M3	0	0	0	1	64	198.0	102.0	100.0	167.0	2.1	1.9
M4	0	0	0	1	61	236.0	120.0	123.0	223.0	2.6	2.3
M5	0	0	0	1	61	195.0	109.0	104.0	171.0	2.3	2.0
M6	0	0	0	1	52	180.0	85.0	95.0	143.0	1.9	1.9
M7	0	0	0	1	63	173.0	113.0	84.0	171.0	2.2	2.0
M8	0	0	0	1	61	248.0	98.0	110.0	239.0	2.5	2.0
M9	0	0	0	1	70	289.0	134.0	139.0	249.0	3.0	2.1
M10	0	0	0	1	73	237.0	129.0	119.0	208.0	2.8	2.3
M11	0	0	0	1	73	257.0	135.0	121.0	220.0	3.5	2.6
M12	0	0	0	1	58	186.0	115.0	97.0	205.0	2.7	2.0
M13	0	0	0	1	71	252.0	112.0	113.0	222.5	2.9	2.4
M14	0	0	0	1	71	246.0	118.0	107.0	224.0	3.0	2.5
M15	0	0	0	1	68	222.0	138.0	102.0	139.0	2.7	2.2
M16	0	0	0	1	69	243.0	125.0	119.0	180.0	3.0	2.8
M17	0	0	0	1	66	309.0	117.0	153.0	183.0	2.5	2.3
M18	0	0	0	1	67	295.0	125.5	167.0	182.0	2.7	2.5
M19	0	0	0	1	64	276.0	123.0	113.0	147.0	3.1	2.4
M20	0	0	0	1	62	277.0	121.0	127.0	174.0	3.0	2.4

Appendix 2. Continued

Individual	STEM	STEMHEI	STEMDIA	LAMUND	PLEATS	LAMLEN	LAMWID	LAMWB	PETLEN	PETWID	PETDEP
M21	0	0	0	1	65	253.0	109.0	129.0	186.0	2.4	2.0
M22	0	0	0	1	65	250.0	148.0	128.0	216.0	3.0	2.1
M23	0	0	0	1	67	315.0	113.0	136.0	247.0	3.5	2.5
M24	0	0	0	1	67	221.0	130.0	123.0	237.0	3.0	2.4
M25	0	0	0	1	62	221.0	119.0	120.0	142.0	2.1	1.8
M26	0	0	0	1	58	231.0	97.0	109.0	183.0	2.1	2.0
M27	0	0	0	1	59	227.0	89.0	107.0	134.0	2.1	1.9
M28	0	0	0	1	74	255.0	129.0	146.0	131.0	2.7	2.0
M29	0	0	0	1	61	195.0	117.0	97.0	82.0	2.1	1.9
M30	0	0	0	1	62	201.0	99.0	118.0	107.0	2.9	2.1
M31	0	0	0	1	58	224.0	103.0	94.0	89.0	2.5	2.0
M32	0	0	0	1	62	226.0	121.0	117.0	120.0	2.7	2.0
M33	0	0	0	1	58	237.5	102.5	134.0	183.5	2.7	2.5
M34	0	0	0	1	57	194.5	71.5	118.0	160.0	1.9	1.8
M35	0	0	0	1	54	198.0	73.0	103.0	135.0	2.4	2.2
M36	0	0	0	1	60	231.0	101.0	115.0	196.0	2.8	2.5
M37	0	0	0	1	53	194.0	74.0	96.0	124.0	1.8	1.5
M38	0	0	0	1	68	243.0	112.0	144.0	197.0	2.4	2.1
M39	0	0	0	1	59	191.5	100.0	103.0	158.0	2.2	1.9
M40	0	0	0	1	64	221.0	100.0	132.0	232.0	2.5	2.0
P1	1	43	49	0	66	293.0	112.0	156.0	157.0	3.0	2.0
P2	1	176	48	0	60	208.0	105.0	126.0	92.0	5.0	3.0
P3	1	88	50	0	68	254.0	108.0	123.0	239.0	2.4	1.8
P4	1	131	41	0	58	225.0	81.0	127.0	128.0	2.0	1.2
P5	1	227	38	0	54	261.0	84.0	148.0	195.0	2.3	1.7
P6	1	25	51	0	31	265.0	64.0	121.0	224.0	2.0	1.8
P7	1	35	57	0	76	349.0	89.0	124.0	303.0	3.1	2.6
P8	1	70	49	0	63	268.0	94.0	133.0	217.0	2.5	1.8
P9	1	90	52	0	62	295.0	77.0	112.0	211.0	1.9	1.7
P10	1	62	62	0	58	199.0	77.0	87.0	169.0	1.7	1.8
P11	1	87	105	0	62	242.0	92.0	120.0	224.0	2.5	2.5
P12	1	74	33	0	62	208.0	81.0	97.0	138.0	2.0	1.5
P13	1	50	58	0	62	162.0	80.0	76.0	163.0	1.4	1.1
P14	1	75	46	0	60	211.0	79.0	94.0	188.0	1.7	1.5
P15	1	164	38	0	60	243.0	96.0	131.0	151.0	2.1	1.9
P16	1	181	46	0	58	216.0	92.0	103.0	124.0	1.9	1.6
P17	1	255	42	0	64	235.0	91.0	115.0	204.0	2.1	1.9
P18	0	0	0	0	63	260.0	87.0	103.0	246.0	2.0	1.7
P19	1	58	64	0	62	261.0	98.0	122.0	216.0	2.2	1.6

Appendix 2. *Continued*

Individual	STEM	STEMHEI	STEMDIA	LAMUND	PLEATS	LAMLEN	LAMWID	LAMWB	PETLEN	PETWID	PETDEP
P20	0	0	0	0	60	237.0	80.0	125.0	144.0	1.6	1.8
P21	0	0	0	0	55	275.0	96.0	168.0	287.0	2.1	1.7
P22	1	145	43	0	56	213.0	78.0	121.0	163.0	1.5	1.9
P23	1	118	55	0	62	230.0	78.0	102.0	93.0	2.0	1.7
P24	1	96	39	0	48	196.0	69.0	112.0	107.0	1.5	1.7
P25	1	126	16	0	69	258.0	108.0	129.0	121.0	2.6	2.1
P26	1	145	49	0	65	266.0	109.0	111.0	163.0	3.0	3.0
P27	1	72	45	0	76	243.0	107.0	120.0	169.0	2.8	2.2
P28	1	106	34	0	62	244.0	113.0	104.0	119.0	2.5	2.0
P29	1	285	39	0	67	214.0	97.0	89.0	120.0	2.4	2.0
P30	1	193	39	0	67	250.0	111.0	104.0	120.0	2.1	2.0
P31	1	122	45	0	59	266.0	95.0	115.0	130.0	2.5	2.3
P32	1	520	48	0	67	246.0	98.0	119.0	127.0	2.5	2.0

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.

Sample	Population	Species	Taxonomic authority	Collector and herbarium information	Locality information	PRK	RPB2
J_lanceolata_1.1	1	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.	Look 020/SINU	Sungai Lalang Forest Reserve, Hulu Langat, Selangor	KF991672	KF991836
J_lanceolata_1.2	1	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			*	KF991838
J_lanceolata_1.3	1	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			KF991674	KF991839
J_lanceolata_1.4	1	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			KF991675	KF991840
J_lanceolata_1.5	1	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			KF991676	KF991841
J_lanceolata_1.6	1	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			KF991677	KF991842
J_lanceolata_1.7	1	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			KF991678	KF991843
J_lanceolata_1.8	1	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			KF991679	KF991844
J_lanceolata_1.9	1	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			KF991680	KF991845
J_lanceolata_1.10	1	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			KF991673	KF991837
J_lanceolata_2.3	2	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.	Look 062/SINU	Gunung Angsi Forest Reserve, Hulu Bendul, Kuala Pilah, Negeri Sembilan	*	KF991849
J_lanceolata_2.4	2	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			KF991685	KF991850
J_lanceolata_2.5	2	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			*	KF991851
J_lanceolata_2.6	2	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			*	KF991852
J_lanceolata_2.7	2	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			KF991686	KF991853
J_lanceolata_2.8	2	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			*	KF991854
J_lanceolata_2.9	2	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			*	KF991855
J_lanceolata_2.10	2	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			*	KF991846
J_lanceolata_2.11	2	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			*	KF991847
J_lanceolata_2.12	2	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			KF991681	KF991848
J_lanceolata_2.17	2	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			KF991682	*
J_lanceolata_2.23	2	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			KF991683	*
J_lanceolata_2.29	2	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			KF991684	*
J_lanceolata_3.1	3	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.	Look 405/SINU	33 Mile Post Point along Jerantut-Benta Road, Jerantut, Pahang	KF991687	KF991856
J_lanceolata_3.2	3	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			KF991689	KF991857
J_lanceolata_3.3	3	<i>Johannesteijsmannia lanceolata</i>	J. Dransf.			KF991690	KF991858

Appendix 3. *Continued*

Sample	Population	Species	Taxonomic authority	Collector and herbarium information	Locality information	PRK	RPB2
J_lanceolata_3.4	3	<i>Johannesteijsmannia lanceolata</i>	J.Dransf.			*	KF991859
J_lanceolata_3.5	3	<i>Johannesteijsmannia lanceolata</i>	J.Dransf.			KF991691	KF991860
J_lanceolata_3.6	3	<i>Johannesteijsmannia lanceolata</i>	J.Dransf.			KF991692	KF991861
J_lanceolata_3.7	3	<i>Johannesteijsmannia lanceolata</i>	J.Dransf.			KF991693	KF991862
J_lanceolata_3.8	3	<i>Johannesteijsmannia lanceolata</i>	J.Dransf.			KF991694	KF991863
J_lanceolata_3.9	3	<i>Johannesteijsmannia lanceolata</i>	J.Dransf.			KF991695	KF991864
J_lanceolata_3.10	3	<i>Johannesteijsmannia lanceolata</i>	J.Dransf.	Look	Krau Wildlife Reserve, Kuala Krau, Temerloh, Pahang	KF991688	*
J_lanceolata_4.1	4	<i>Johannesteijsmannia lanceolata</i>	J.Dransf.	Look 436/SINU		KF991696	*
J_lanceolata_4.2	4	<i>Johannesteijsmannia lanceolata</i>	J.Dransf.			KF991698	*
J_lanceolata_4.3	4	<i>Johannesteijsmannia lanceolata</i>	J.Dransf.			KF991699	*
J_lanceolata_4.4	4	<i>Johannesteijsmannia lanceolata</i>	J.Dransf.			KF991700	*
J_lanceolata_4.5	4	<i>Johannesteijsmannia lanceolata</i>	J.Dransf.			KF991701	*
J_lanceolata_4.6	4	<i>Johannesteijsmannia lanceolata</i>	J.Dransf.			KF991702	KF991869
J_lanceolata_4.7	4	<i>Johannesteijsmannia lanceolata</i>	J.Dransf.			KF991703	KF991870
J_lanceolata_4.8	4	<i>Johannesteijsmannia lanceolata</i>	J.Dransf.			KF991704	*
J_lanceolata_4.9	4	<i>Johannesteijsmannia lanceolata</i>	J.Dransf.			KF991705	KF991871
J_lanceolata_4.10	4	<i>Johannesteijsmannia lanceolata</i>	J.Dransf.			KF991697	KF991865
J_lanceolata_4.14	4	<i>Johannesteijsmannia lanceolata</i>	J.Dransf.			*	KF991866
J_lanceolata_4.15	4	<i>Johannesteijsmannia lanceolata</i>	J.Dransf.			*	KF991867
J_lanceolata_4.20	4	<i>Johannesteijsmannia lanceolata</i>	J.Dransf.			*	KF991868
J_altifrons_1.1	1	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore	Look 084/SINU	Gunung Janing, Endau-Rompin State Park, Johor	KF991706	KF991872
J_altifrons_1.2	1	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore			KF991707	KF991874
J_altifrons_1.3	1	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore			KF991708	KF991875
J_altifrons_1.4	1	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore			KF991709	KF991876
J_altifrons_1.5	1	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore			KF991710	KF991877
J_altifrons_1.6	1	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore			KF991711	KF991878

Appendix 3. Continued

Sample	Population	Species	Taxonomic authority	Collector and herbarium information	Locality information	PRK	RPB2
J_altifrons_1.7	1	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991712	KF991879
J_altifrons_1.8	1	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991713	KF991880
J_altifrons_1.9	1	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991714	KF991881
J_altifrons_1.10	1	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			*	KF991873
J_altifrons_2.1	2	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore	Look 104/SINU	Gunung Eedang, Kampung Tambun, Kawasan Sukhirin, Narathiwat, Thailand	KF991715	*
J_altifrons_2.2	2	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991717	*
J_altifrons_2.3	2	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991718	KF991883
J_altifrons_2.4	2	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991719	*
J_altifrons_2.5	2	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991720	*
J_altifrons_2.6	2	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991721	*
J_altifrons_2.7	2	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991722	*
J_altifrons_2.8	2	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991723	*
J_altifrons_2.9	2	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991724	*
J_altifrons_2.10	2	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991716	*
J_altifrons_2.11	2	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			*	KF991882
J_altifrons_3.1	3	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore	Look 135/SINU	Sungai Lalang Forest Reserve, Hulu Langat, Selangor	*	KF991884

Appendix 3. *Continued*

Sample	Population	Species	Taxonomic authority	Collector and herbarium information	Locality information	PRK	RPB2
J_altifrons_3.2	3	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			*	KF991886
J_altifrons_3.3	3	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991726	KF991887
J_altifrons_3.4	3	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991727	KF991888
J_altifrons_3.5	3	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991728	KF991889
J_altifrons_3.6	3	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991729	KF991890
J_altifrons_3.7	3	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991730	KF991891
J_altifrons_3.8	3	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991731	KF991892
J_altifrons_3.9	3	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991732	KF991893
J_altifrons_3.10	3	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991725	KF991885
J_altifrons_4.1	4	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore	Look 161/SINU	Bukit Tambi, Bako National Park, Kuching, Sarawak	KF991733	KF991894
J_altifrons_4.2	4	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991735	KF991895
J_altifrons_4.3	4	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991736	KF991896
J_altifrons_4.4	4	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991737	KF991897
J_altifrons_4.5	4	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991738	KF991898
J_altifrons_4.6	4	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991739	KF991899
J_altifrons_4.7	4	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991740	KF991900
J_altifrons_4.8	4	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991741	KF991901
J_altifrons_4.9	4	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991742	*

Appendix 3. Continued

Sample	Population	Species	Taxonomic authority	Collector and herbarium information	Locality information	PRK	RPB2
J_altifrons_4.10	4	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991734	*
J_altifrons_5.1	5	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore	Look 170/SINU	Government Land, next to Compartment 58, Batu Papan Forest Reserve, Gua Musang, Kelantan	KF991743	KF991902
J_altifrons_5.2	5	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			*	KF991904
J_altifrons_5.3	5	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991745	KF991905
J_altifrons_5.4	5	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991746	KF991906
J_altifrons_5.5	5	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991747	KF991907
J_altifrons_5.6	5	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991748	KF991908
J_altifrons_5.7	5	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			*	KF991909
J_altifrons_5.8	5	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991749	KF991910
J_altifrons_5.9	5	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			*	KF991911
J_altifrons_5.10	5	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991744	KF991903
J_altifrons_6.1	6	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore	Look 179/SINU	Compartment 13, Sungai Durian Forest Reserve, Kuala Krai, Kelantan	KF991750	KF991912
J_altifrons_6.2	6	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			*	KF991914
J_altifrons_6.3	6	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991752	KF991915
J_altifrons_6.4	6	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991753	KF991916

Appendix 3. *Continued*

Sample	Population	Species	Taxonomic authority	Collector and herbarium information	Locality information	PRK	RPB2
J_altifrons_6.5	6	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore			KF991754	KF991917
J_altifrons_6.6	6	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore			KF991755	KF991918
J_altifrons_6.7	6	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore			*	KF991919
J_altifrons_6.8	6	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore			KF991756	KF991920
J_altifrons_6.9	6	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore			*	KF991921
J_altifrons_6.10	6	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore			KF991751	KF991913
J_altifrons_7.1	7	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore	Look 414/SINU	Compartment 72, Sungai Nipah Forest Reserve, Kemaman, Terengganu	KF991757	KF991922
J_altifrons_7.2	7	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore			KF991759	KF991924
J_altifrons_7.3	7	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore			KF991760	KF991925
J_altifrons_7.4	7	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore			KF991761	KF991926
J_altifrons_7.5	7	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore			KF991762	KF991927
J_altifrons_7.6	7	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore			KF991763	KF991928
J_altifrons_7.7	7	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore			KF991764	KF991929
J_altifrons_7.8	7	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore			KF991765	KF991930
J_altifrons_7.9	7	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore			KF991766	KF991931
J_altifrons_7.10	7	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore			KF991758	KF991923
J_altifrons_8.1	8	<i>Johannesteijsmannia altifrons</i>	(Rchb.f. & Zoll.) H.E.Moore	Look 429/SINU	Belum Forest, Grik, Perak	KF991767	KF991932

Appendix 3. Continued

Sample	Population	Species	Taxonomic authority	Collector and herbarium information	Locality information	PRK	RPB2
J_altifrons_8.2	8	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991769	KF991934
J_altifrons_8.3	8	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991770	KF991935
J_altifrons_8.4	8	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991771	KF991936
J_altifrons_8.5	8	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991772	KF991937
J_altifrons_8.6	8	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991773	KF991938
J_altifrons_8.7	8	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991774	KF991939
J_altifrons_8.8	8	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991775	KF991940
J_altifrons_8.9	8	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991776	KF991941
J_altifrons_8.10	8	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991768	KF991933
J_altifrons_9.1	9	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore	Look 443/SINU	Berkelah Forest Reserve, Jerantut, Pahang	KF991777	KF991942
J_altifrons_9.2	9	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991779	KF991944
J_altifrons_9.3	9	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991780	KF991945
J_altifrons_9.4	9	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991781	KF991946
J_altifrons_9.5	9	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991782	KF991947
J_altifrons_9.6	9	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991783	KF991948
J_altifrons_9.7	9	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991784	KF991949
J_altifrons_9.8	9	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991785	KF991950
J_altifrons_9.9	9	<i>Johannesteijsmannia altifrons</i>	(Rechb.f. & Zoll.) H.E.Moore			KF991786	KF991951

Appendix 3. *Continued*

Sample	Population	Species	Taxonomic authority	Collector and herbarium information	Locality information	PRK	RPB2
J_ altifrons_9.10	9	<i>Johannesteijsmannia altifrons</i>	(Rehb.f. & Zoll.) H.E.Moore			KF991778	KF991943
J_ perakensis_1.1	1	<i>Johannesteijsmannia perakensis</i>	J.Dransf.	Look 035/SINU	Kledang-Saiong Forest Reserve, Kuala Kangsar, Perak	KF991952	KF991787
J_ perakensis_1.2	1	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991954	KF991789
J_ perakensis_1.3	1	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			*	KF991790
J_ perakensis_1.4	1	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991955	KF991791
J_ perakensis_1.5	1	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991956	KF991792
J_ perakensis_1.6	1	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991957	*
J_ perakensis_1.7	1	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991958	KF991793
J_ perakensis_1.8	1	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991959	KF991794
J_ perakensis_1.9	1	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991960	KF991795
J_ perakensis_1.10	1	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991953	KF991788
J_ perakensis_2.1	2	<i>Johannesteijsmannia perakensis</i>	J.Dransf.	Look 040/SINU	Compartment 44A, Gunung Bubu, Bubu Forest Reserve, Kuala Kangsar, Perak	KF991961	KF991796
J_ perakensis_2.2	2	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991963	KF991797
J_ perakensis_2.3	2	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991964	*
J_ perakensis_2.4	2	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991965	KF991798
J_ perakensis_2.5	2	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991966	KF991799
J_ perakensis_2.6	2	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991967	KF991800
J_ perakensis_2.7	2	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			*	KF991801
J_ perakensis_2.8	2	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991968	KF991802
J_ perakensis_2.9	2	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991969	KF991803
J_ perakensis_2.10	2	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991962	*
J_ perakensis_3.1	3	<i>Johannesteijsmannia perakensis</i>	J.Dransf.	Look 147/SINU	Compartment 55, Gunung Bongsu Forest Reserve, Kulim, Kedah	KF991970	KF991804
J_ perakensis_3.2	3	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991972	KF991805
J_ perakensis_3.3	3	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991973	*
J_ perakensis_3.4	3	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991974	KF991806
J_ perakensis_3.5	3	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991975	KF991807

Appendix 3. Continued

Sample	Population	Species	Taxonomic authority	Collector and herbarium information	Locality information	PRK	RPB2
J_perakensis_3.6	3	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991976	KF991808
J_perakensis_3.7	3	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991977	KF991809
J_perakensis_3.8	3	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991978	KF991810
J_perakensis_3.9	3	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991979	KF991811
J_perakensis_3.10	3	<i>Johannesteijsmannia perakensis</i>	J.Dransf.			KF991971	*
J_magnifica_1.1	1	<i>Johannesteijsmannia magnifica</i>	J.Dransf.	Look 070/SINU	Berembun Forest Reserve, Kuala Klawang, Jelebu, Negeri Sembilan	KF991980	KF991812
J_magnifica_1.2	1	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF991982	KF991814
J_magnifica_1.3	1	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF991983	KF991815
J_magnifica_1.4	1	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF991984	KF991816
J_magnifica_1.5	1	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF991985	KF991817
J_magnifica_1.6	1	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF991986	KF991818
J_magnifica_1.7	1	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF991987	KF991819
J_magnifica_1.8	1	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF991988	*
J_magnifica_1.9	1	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF991989	KF991820
J_magnifica_1.10	1	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF991981	KF991813
J_magnifica_2.1	2	<i>Johannesteijsmannia magnifica</i>	J.Dransf.	Look 130/SINU	26 Miles, Kampung Orang Asli, Sungai Lalang Forest Reserve, Hulu Langat, Selangor	KF991990	*
J_magnifica_2.2	2	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF991992	*
J_magnifica_2.3	2	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF991993	KF991824
J_magnifica_2.4	2	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF991994	*
J_magnifica_2.5	2	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF991995	*
J_magnifica_2.6	2	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF991996	KF991825
J_magnifica_2.7	2	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF991997	*
J_magnifica_2.8	2	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF991998	*
J_magnifica_2.9	2	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF991999	*
J_magnifica_2.10	2	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF991991	*
J_magnifica_2.11	2	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			*	KF991821
J_magnifica_2.13	2	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			*	KF991822
J_magnifica_2.15	2	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			*	KF991823

Appendix 3. *Continued*

Sample	Population	Species	Taxonomic authority	Collector and herbarium information	Locality information	PRK	RPB2
J_magnifica_3.1	3	<i>Johannesteijsmannia magnifica</i>	J.Dransf.	Look 421/SINU	Compartment 78/79, Bukit Kinta Forest Reserve, Kinta, Perak	KF992000	KF991826
J_magnifica_3.2	3	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF992002	KF991828
J_magnifica_3.3	3	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF992003	KF991829
J_magnifica_3.4	3	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF992004	KF991830
J_magnifica_3.5	3	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF992005	KF991831
J_magnifica_3.6	3	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF992006	KF991832
J_magnifica_3.7	3	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF992007	KF991833
J_magnifica_3.8	3	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF992008	KF991834
J_magnifica_3.9	3	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF992009	KF991835
J_magnifica_3.10	3	<i>Johannesteijsmannia magnifica</i>	J.Dransf.			KF992001	KF991827

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.