Sympatric speciation in palms on an oceanic island

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The origin of species diversity has challenged biologists for over two centuries. Allopatric speciation, the divergence of species resulting from geographical isolation, is well documented[1]. However, sympatric speciation, divergence without geographical isolation, is highly controversial[2]. Claims of sympatric speciation must demonstrate species sympatry, sister relationships, reproductive isolation, and that an earlier allopatric phase is highly unlikely[1]. Here we provide clear support for sympatric speciation in a case study of two species of palm (Arecaceae) on an oceanic island. A large dated phylogenetic tree shows that the two species of *Howea*, endemic to the remote Lord Howe Island, are sister taxa and diverged from each other well after the island was formed 6.9 million years ago[3]. During fieldwork, we found a substantial disjunction in flowering time that is correlated with soil preference. In addition, a genome scan[4,5] indicates that few genetic loci are more divergent between the two species than expected under neutrality, a finding consistent with models of sympatric speciation involving disruptive/divergent selection[2]. This case study of sympatric speciation in plants provides an opportunity for refining theoretical models on the origin of species, and new impetus for exploring putative plant and animal examples on oceanic islands.

Speciation, the division of populations into evolutionarily independent units, involves genetic separation and phenotypic differentiation. Genetic divergence following geographic isolation gives rise to allopatric speciation: "the conceptual rationale is simply that, given enough time, speciation is an inevitable consequence of populations evolving in allopatry"[6]. Numerous empirical examples support this uncontroversial scenario[1]. In theory, however, populations can become genetically isolated without geographical separation, resulting in sympatric speciation, a much more contentious model. Sympatric speciation is more strictly defined as the emergence of two species from a population in which mating has been random with respect to the place of birth of the mating partners[2].

Mathematical models have shown that sympatric speciation is possible[2,7–10], but very few examples have been documented in nature[11,12]. Cichlid fish seem to have radiated sympatrically in African crater lakes. Molecular phylogenetic analyses show that the fish species in each lake share a common ancestor, with sexual selection and ecology possibly driving speciation[13]. Second, races of apple and hawthorn maggot have shifted to different hosts in sympatry and differ in reproductive behaviour and breeding time[14]. Third, a genetic study of African indigobirds, which are host-specific brood parasites, showed that they might have recently speciated sympatrically after new hosts were colonized[15]. These examples are all from animal taxa with relatively large continental geographic distributions. This leaves the door open to controversy, given that truly convincing cases of sympatric speciation must involve biogeographic and phylogenetic histories that make the existence of an allopatric phase highly unlikely[1]. For this reason,

we focused on a plant species-pair confined to a remote oceanic island.

Lord Howe Island (Fig. 1a) is a small subtropical island of less than 12 km[2], situated 580 km off the eastern coast of Australia. The island was formed by volcanic activity 6.4–6.9 million years (Myr) ago[3]. Lord Howe Island is the most southerly member of a 1,000-km chain of nine underwater volcanoes along the Lord Howe Rise. The closest link in the Lord Howe Island chain is Elizabeth Reef, 160 km to the north; this seamount was an island 10.2 Myr ago[3]. Lord Howe Island

Figure 1 | **Lord Howe Island and its endemic palms. a**, Lord Howe Island is a World Heritage Site, and a permanent park preserve now protects 70% of the island. The waters surrounding Lord Howe Island are protected as a marine park, which also holds the world's southernmost coral reef. The island is inhabited by approximately 300 residents, and less than 20% of the vegetation has been disturbed. **b**, The kentia or thatch palm, *Howea forsteriana*, is characterized by multiple spikes in each inflorescence and has straight leaves with drooping leaflets. **c**, The curly palm, *H. belmoreana*, bears a single spike in each inflorescence and has recurved leaves with ascending leaflets.

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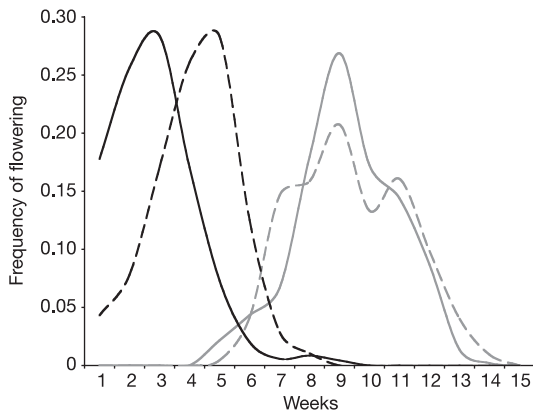
Figure 2 | Flowering phenology for each *Howea* species. *H. belmoreana* is shown in grey ($n = 198$), *H. forsteriana* in black ($n = 177$), with male (solid line) and female (dotted line) phases (see Methods). The flowering times of the two species are strongly displaced. In addition, both species are significantly different in their sexual synchrony index (SI; $F_{1,222} = 27.26$, $P < 10^{-4}$). The SI is not significantly different from zero ($n = 132$, $t = -0.30$ weeks (t-test), $P = 0.18$) and does not differ among sites of *H. belmoreana* ($F_{8,131} = 1.54$, $P = 0.15$), whereas *H. forsteriana* is strongly protandrous (mean SI = 1.3 weeks, $n = 92$, $t = 6.75$, $P < 10^{-4}$) and there are significant differences among sites ($F_{8,83} = 1.96$, $P = 0.0619$).

itself has eroded rapidly and will be awash within 200,000 years. Apart from Ball's Pyramid, a precipitous sea stack 23 km southeast of Lord Howe Island that supports only limited plant life, there are no islands nearby, and Australia is the nearest land mass. However, the indigenous vascular flora of Lord Howe Island has greater affinities with New Zealand and New Caledonia than with Australia. Of its 241 plant species, almost half are endemic, and the terrestrial fauna of the island shows similar levels of endemism. Lord Howe Island represents an ideal location to study sympatric speciation because it has long been isolated, is of known age and is so small that geographical isolation on the island cannot realistically occur[3].

The palm family is represented on Lord Howe Island by four species in three strictly endemic genera. The two species of *Howea*, *H. belmoreana* and *H. forsteriana*, are extremely abundant, occurring in more than 70% of the island's vegetation[16]. *Howea forsteriana*, the kentia palm, is one of the most widely traded houseplants in the world and is worth over €7 million per year in the Dutch horticultural industry alone. The two species of *Howea* display striking morphological differences and their taxonomic status is indisputable[17] (Fig. 1b, c). They occur sympatrically in numerous places on Lord Howe Island[16], and yet putative hybrids have only rarely been reported[18]; our thorough fieldwork identified only five specimens

with intermediate morphologies. We have also confirmed that both species are diploid ($2n = 32$) using conventional cytological techniques, thereby excluding polyploid speciation[19].

We have produced the most comprehensive DNA-based phylogenetic tree for the largest subfamily of palms (Arecoideae), comprising 132 taxa, including all 67 genera of the Indo-Pacific Areceae[20]. These data strongly support the monophyly of *Howea* and a sister relationship to the monotypic Australian genus *Laccospadix*. Correcting for molecular rate heterogeneity across lineages, we have dated this tree using four calibration points simultaneously, all independent from Lord Howe Island. Using two different molecular dating methods[21,22], we estimated the split between *Howea* and *Laccospadix* to be 4.57–5.53 Myr old, and that the two *Howea* species diverged 1.92 ± 0.53 Myr ago (nonparametric rate smoothing (NPRS); Table 1) or just less than 1 Myr ago (bayesian; Table 1), long after Lord Howe Island was formed. Other dates in the tree are also consistent with geological history, including the root nodes of the other two endemic Lord Howe Island palm genera, *Hedyscepe* and *Lepidorrhachis*, and the root node of *Carpoxylon*, which is younger than the age of Vanuatu[23] on which it is endemic (Table 1).

During fieldwork, we monitored both *Howea* species throughout the flowering season. Phenological data indicate that the species are reproductively isolated, with *H. forsteriana* flowering before *H. belmoreana*. The peak flowering of each species is separated by approximately six weeks and has limited overlap (Fig. 2). *Howea forsteriana* is protandrous at the population level, with male flowering peaking two weeks before female receptivity, whereas *H. belmoreana* is synchronous (Fig. 2). Notably, when *H. forsteriana* occurs on volcanic rather than calcareous substrates, asynchronous maturation is not observed (Supplementary Information; $t = 0.49$ (t-test), $n = 12$, $P = 0.63$). Thus, flowering-time differences seem to be directly influenced by substrate-induced physiological changes. We also found that *Howea* is wind-pollinated, a rare syndrome in palms (contrary to popular belief), and complete exclusion experiments demonstrated the absence of apomixis in both species.

The distributions of *H. forsteriana* and *H. belmoreana* are also dependent on soil pH (Fig. 3). *Howea belmoreana* is restricted to neutral and acidic soils, whereas *H. forsteriana* prefers calcarenite, a recent basic sedimentary formation that dominates low-lying parts of the island[3]. The same pattern is observed for both adults and juveniles ($r^2 = 0.79$, $n = 22$ sites, $P < 10^{-4}$ for *H. forsteriana*; $r^2 = 0.69$, $n = 43$, $P < 10^{-4}$ for *H. belmoreana*). Despite this preference, both species occur sympatrically in 11 out of the 55 quadrats that contain palms (see Methods).

Consistent with sympatric speciation, genetic divergence (F_{ST}) within the genome, estimated using 274 polymorphic amplified fragment-length polymorphism (AFLP) loci, follows an L-shaped distribution, with most loci showing low F_{ST} and only a small number

Table 1 | Ages for root nodes (in Myr) calculated from molecular phylogenetic trees

Taxa	Node number*	Distribution	Node age ± s.d. (NPRS)	Node age ± s.d. (bayesian)
Acanthophoenix/Tectiphiala	1	Mascarenes†	7.61 ± 1.70	6.52 ± 1.10
Dictyosperma (hurricane palm)	2	Mascarenes‡	7.75 ± 1.83	6.60 ± 1.22
Hyophorbe (bottle palm)	3	Mascarenes‡	7.75 ± 0.02	7.45 ± 0.38
Palms	4	Widespread§	88.93 ± 9.38	85.73 ± 2.20
Carpoxylon	5	Vanuatu‖	7.07 ± 2.05	11.98 ± 5.36
Hedyscepe (big mountain palm)	6	LHI	6.66 ± 2.45	8.24 ± 4.30
Lepidorrhachis (little mountain palm)	7	LHI	7.77 ± 3.07	4.62 ± 3.28
Howea	8	LHI	4.57 ± 1.45	5.53 ± 2.89
Howea belmoreana (curly palm)/*Howea forsteriana* (kentia palm) split	9	LHI	1.92 ± 0.53	<1.00¶

LHI, Lord Howe Island.
*Nodes 1–4 are calibration points. See also Supplementary Information.
†*Acanthophoenix* occurs on La Réunion (2 Myr) and Mauritius (7.8 Myr); *Tectiphiala* occurs on Mauritius only.
‡*Dictyosperma* and *Hyophorbe* occur on La Réunion, Mauritius and Rodrigues.
§Santonian fossil, *Sabalites magothiensis*, 83.5 Myr old (ref. 30).
‖The age of Vanuatu is about 10 Myr, although the exact figure is disputed[23]. Therefore, we did not use this point as a calibration; it is given here for comparative purposes only.
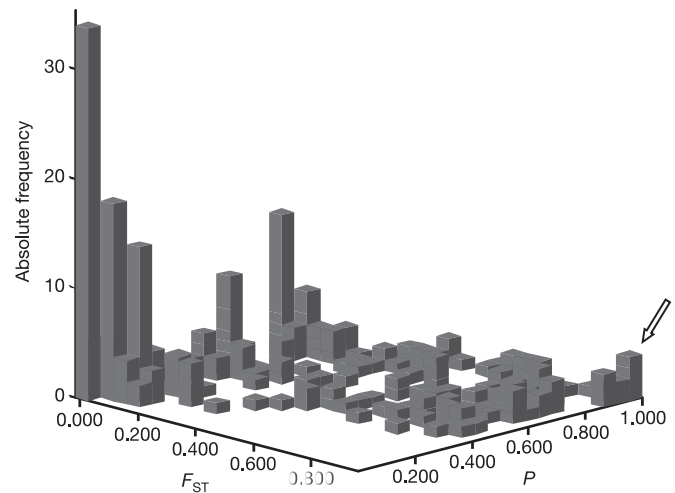¶Age under the 1-Myr detection level in the bayesian dating calculation of this data set.
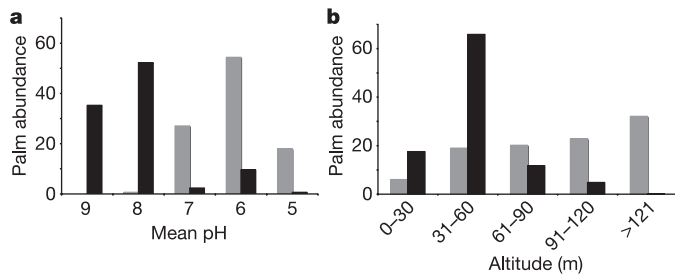
Figure 3 | Distribution of *H. forsteriana* and *H. belmoreana* according to mean soil pH and elevation. Number of palm trees; *H. forsteriana* is shown in black ($n = 1,677$) and *H. belmoreana* in grey ($n = 4,542$). **a**, **b**, Distribution according to the mean pH of the soil (**a**) in each quadrat and elevation (**b**). *Howea forsteriana* is found in sites at lower elevation ($P < 3 \times 10^{-4}$) and higher soil pH ($P < 10^{-4}$) than *H. belmoreana*, and is largely restricted to calcarenite. However, both species coexist over a large range of elevations and soil pH.

Figure 4 | AFLP genome scan for species differentiation in *H. belmoreana* and *H. forsteriana*. Histogram shows the frequency distribution of estimates for interspecific genetic divergence (F_{ST}) for 274 AFLP loci. Frequencies are on the vertical axis; F_{ST} and the probability of departure from the null-hypothesis of neutrality[24] are on the horizontal axes. In the upper tail of the F_{ST} distribution, four loci that depart from neutral expectations at the 0.95 level are indicated by an arrow. These four loci have equal probabilities as all four are fixed in the two species.

of loci showing high levels of divergence (Fig. 4). Accordingly, the median of F_{ST} is much lower than the mean (median 0.131; mean 0.307 ± 0.020). In the upper tail of the distribution, only four of these AFLP loci differ more strongly between the two species than expected under neutrality[5,24] (Fig. 4). This signature of species divergence is completely different from that of allopatric speciation, for which genetic differences are expected to accumulate throughout the entire genome[25]. The four loci were the only markers that were fixed in the two species ($P > 0.95$; Fig. 4), resulting in a experiment-wide significance level for rejection of the null-hypothesis of neutrality of $P < 10^{-5}$: these loci are those most likely to be linked to genes subject to divergent selection during sympatric speciation.

Thus, our phylogenetic, ecological and genomic data are consistent with the following scenario. The ancestor of *Howea* reached Lord Howe Island, most likely from Australia, as long as 4.5–5.5 Myr ago. More recently, *H. forsteriana* diverged from its sister species (an ancestor of *H. belmoreana*) by colonizing widespread lowland calcarenite deposits. Calcarenite dates from the mid-Pleistocene[26], which corresponds well to the age of the split between the two *Howea* species recovered from the molecular clocks (Table 1). The absence of protandry in *H. forsteriana* on less basic soils indicates that the conspicuous flowering time difference may have arisen as a physiological response to a new substrate, thus introducing a bias in random mating and kicking-off speciation. However, despite their striking edaphic preferences, it is very unlikely that the two species have ever been truly spatially isolated from each other, given that Lord Howe Island is so small, that volcanic and calcarenite substrates are highly interdigitated, that both species co-occur in ~20% of their modern distribution range and that both are wind-pollinated. The role of other islands on the Lord Howe Rise is not relevant to the speciation event because all of them eroded long before the *Howea* species diverged from each other. The role of the nearest landmasses, Australia, New Caledonia and New Zealand, is equally unlikely to be involved in the speciation of *Howea*, as extensive exploration of the Indo-Pacific palm flora has shown that *Howea* is strictly endemic to Lord Howe Island.

Current models of sympatric speciation invoke either one 'magic trait' that is both subject to disruptive selection and controls non-random mating, or linkage disequilibrium between genes controlling assortative mating and those conferring novel adaptation[2,7,9,27]. We do not know which model is more likely in the case of *Howea*. Changes in flowering time may have arisen as a plastic response to exogenous stress on calcarenite. In this scenario, heritable changes in flowering time may have been induced after the speciation event was complete. Alternatively, speciation may have been facilitated by linkage disequilibrium between genes controlling adaptation to calcarenite and those controlling flowering time. Both traits differ

between the two palms (Figs 2, 3). In any case, our data are consistent with models of sympatric speciation involving disruptive/divergent selection on a limited number of genes[2,7,9] (Fig. 4). The data also indicate that the gene pools of these wind-pollinated species are extremely homogeneous, with only 5% of molecular variance between sampled localities for each species (analysis of molecular variance, AMOVA). Hence, mating within the ancestral homogeneous population that gave rise to the two species of *Howea* was indeed random with respect to the place of birth of the mating partners, a characteristic that distinguishes sympatric speciation from other modes of species divergence[2].

METHODS

Phylogenetic analyses and dating. We have sequenced two low-copy nuclear regions (intron 4 of phosphoribulokinase and intron 23 of RNA polymerase II subunit 2) for Arecoideae, with complete genus level sampling for Areceae[20] using polymerase chain reaction (PCR) and DNA automated sequencing (2,464 nucleotides for each of 132 taxa). An initial search using maximum parsimony and 1,000 random taxon-additions and tree bisection-reconnection as implemented in PAUP[28] yielded 2,955 most-parsimonious trees. Using ModelTest we identified HKY85+G as a suitable model of DNA evolution and saved one of the most-parsimonious trees with likelihood branch lengths. Following a likelihood ratio test, a constant molecular clock was rejected ($-$LnL c+ = 20406.36912; $-$LnL c$-$ = 20574.10734; $P < 0.0001$). Therefore, we used both non-parametric rate smoothing (r8s; ref. 21) and bayesian dating methods (DivTime[22]) to generate an ultrametric tree, calibrated using four calibration points simultaneously. The root nodes of three independent lineages endemic to the Indian Ocean Mascarene Islands (*Acanthophoenix/Tectiphiala*, *Dictyosperma* and *Hyophorbe*) were constrained to be no older than 7.8 Myr (ref. 29). The oldest known palm fossil, *Sabalites magothiensis* from the Santonian, provided a minimum age for the root of the tree of 83.5 Myr (ref. 30). Standard deviations were calculated by re-applying the procedure to 100 bootstrapped DNA matrices[21].

Habitat ecology. Seventy-eight non-overlapping quadrats (20×20 m), were generated at random using geographic information system (GIS). Within each quadrat, we recorded the total number of adults and juveniles of each *Howea* species, and the elevation and soil pH. Juveniles were defined as individuals lacking an aerial stem. Soil samples were collected in three places in each quadrat from a depth of 20 cm below the soil surface. The pH of each sample was measured using Inoculo soil pH test kits (EnviroEquip Pty). Differences in pH and elevation between species were tested with a Student's *t*-test.

Phenology. To determine the phenology of *Howea*, nine sites of each species

distributed across the island were visited weekly (September–December 2003). Within each site, 20–25 reproductive specimens were selected. The inflorescences of *Howea* are monoecious and long-lived, with a delay of one year between male and female anthesis, and more than a year until fruit maturation. Thus, each inflorescence persists for four seasons, reaching male anthesis in season 1, female anthesis in season 2, and with fruits ripening through seasons 3 and 4, and any one individual palm bears functionally male, female and fruiting inflorescences simultaneously. For each palm specimen and at each visit, the number of inflorescences in male, female and fruiting phases was counted (A, pre-anthesis; B, anthesis; C, post-anthesis). A synchrony index (SI) was defined at the plant level as the time between the first week of male phase B and the first week of female phase B. An analysis of variance (ANOVA) was used to test for differences in SI between species and sites. Student's *t*-tests were used to determine whether the SI was significantly different from zero for each species. Data were analysed using paired *t*-tests.

Pollination. Flowering spikes nearing female anthesis were subjected to three treatments: (1) insect and wind-borne pollen exclusion (using a paper bag), (2) insect-only exclusion (using a fine-mesh fabric bag), and (3) open pollination. The number of female buds was counted on each spike. Inflorescences were treated well before anthesis, and bags were removed one week after the end of anthesis to prevent a detrimental effect on fruit maturation. Six weeks after the end of female anthesis, the number of developing fruits was counted on each spike. Data were analysed using paired *t*-tests.

Genome scan. AFLP fragments were generated from total DNA using an AFLP plant mapping kit (Applied Biosystems). A total of 48 primer pairs were tested for variability before selecting pairs B13, G7 and Y1 (see manufacturer's protocol). Bands were scored manually using Genotyper 2.0. We estimated F_{ST} values for 274 AFLP bands that matched our polymorphism criteria (Supplementary Information) and compared them to neutral expectations from simulations based on the observed average F_{ST} between the two species. Computer simulations and calculation of significance levels were carried out with the software Dfdist by Beaumont, which uses the method by Beaumont and Nichols[24] adapted to dominant markers. Initial simulations indicated that the results remained robust across a wide range of effective population sizes (N_e) and mutation rates (μ), as already reported by in ref. 24, and the final runs were carried out with 50,000 realizations assuming $N_e = 50,000$ and $\mu = 1 \times 10^{-5}$. Outlier loci were identified in a two-step procedure in which highly divergent loci were selected based on a first round of simulations, the average F_{ST} was re-calculated without them, and a second round of simulations based on the adjusted average F_{ST} was used to identify outliers subject to directional selection. The shape of the F_{ST} distribution was described by comparing the median with the mean.

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