# Case studies and mathematical models of ecological speciation. 2. Palms on an oceanic island

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## Abstract

**A recent study of a pair of sympatric species of palms on the Lord Howe Island is viewed as providing probably one of the most convincing examples of sympatric speciation to date. Here we describe and study a stochastic, individual-based, explicit genetic model tailored for this palms system. Overall, our results show that relatively rapid (< 50 000 generations) colonization of a new ecological niche, and sympatric or parapatric speciation via local adaptation and divergence in flowering periods are theoretically plausible if (i) the number of loci controlling the ecological and flowering period traits is small; (ii) the strength of selection for local adaptation is intermediate; and (iii) an acceleration of flowering by a direct environmental effect associated with the new ecological niche is present. We discuss patterns and time-scales of ecological speciation identified by our model, and we highlight important parameters and features that need to be studied empirically in order to provide information that can be used to improve the biological realism and power of mathematical models of ecological speciation.**

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## Introduction

Savolainen *et al.* (2006a) have recently presented a case study that is viewed by many as probably one of the most convincing examples of sympatric speciation to date. Their study focuses on two sympatric species of palms on an oceanic island that have diverged morphologically by local adaptation to two different ecological niches and have simultaneously diverged in flowering period. According to Savolainen *et al.* (2006a), the new species emerged soon after a new ecological niche became available as a result of the appearance of a new soil type on the island, and its evolution was driven by selection for adaptation to the new ecological niche.

Here we describe an individual-based model tailored for the system studied by Savolainen *et al.* (2006a). The model was designed to study speciation in plants driven by divergent ecological selection for local adaptation occurring simultaneously with divergence in flowering periods. Our

goals are similar to those of the accompanying paper (Gavrilets *et al.* 2007): to use a mathematical model to address a number of questions about ecological (e.g. Mayr 1947; Schluter 2000; Rundle & Nosil 2005; Hendry *et al.* 2007) and sympatric speciation, to identify important parameters, patterns, and time-scales, and to evaluate how common the phenomena observed in the case study might be.

Sympatric speciation is defined as the emergence of new species from a population where mating is random with respect to the birthplace of the mating partners (Gavrilets 2003, 2004). During sympatric speciation, mating may be nonrandom with respect to, for example, genotype, phenotype and culturally-inherited traits. If spatial isolation between diverging populations is not complete and mating is nonrandom with respect to the birthplace of the mating partners (e.g. because of the isolation by distance), then speciation is parapatric.

Analysis of sympatric and parapatric speciation via divergence in flowering period has a long history in theoretical evolutionary biology. In fact, the very first individual-based model of speciation built by Crosby (1970) looked explicitly at this process. In the Crosby

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model the population was subject to disruptive, but spatially homogeneous selection acting on an additive character controlling fertility. Two other independent characters controlled the onset and duration of flowering. Crosby's ground-breaking results demonstrated the possibility of both sympatric and parapatric speciation via divergence in flowering periods driven by selection against hybrids (i.e. reinforcement). Later, Stam (1983) used a combination of simple analytical models and more complex individual-based simulations to show that speciation can be strongly promoted if there are environmentally-induced differences in flowering periods. van Dijk & Bijlsma (1994) extended the work of Crosby (1970) and Stam (1983) in a number of directions. Divergence in flowering was also addressed in other models (e.g. Dickinson & Antonovics 1973; Caisse & Antonovics 1978; Moore 1979, 1981; Spirito 1987; Spirito & Sampogna 1995; reviewed in Chapters 9 and 10 in Gavrilets 2004). Here we extend this previous work by building a more realistic model, which we then study in detail.

### Empirical evidence

In describing empirical evidence we will closely follow Savolainen *et al*. (2006a). Lord Howe Island is a small volcanic island of less than 12 km². It is located in the subtropics around 580 km off the eastern coast of Australia and was formed 6.4–6.9 million years ago. Lord Howe Island belongs to a 1000-km chain of nine underwater volcanoes and is the most southerly of the chain. The closest link in the archipelago is Elizabeth Reef, located 160 km to the north. Elizabeth Reef was an island 10.2 million years ago, but has since eroded and is now beneath the surface. Lord Howe Island is also eroding rapidly and will submerge within 200 000 years. There are no islands nearby Lord Howe Island, with the exception of Ball's Pyramid, a craggy sea stack which only supports limited plant life, located 23 km to the southeast of Lord Howe Island.

The focus of Savolainen *et al*. (2006a) study was on the two species of *Howea*, *H. belmoreana* and *H. forsteriana*, which are extremely abundant, occurring in more than 70% of the island's vegetation. Both species are diploid (2*n* = 32) and wind-pollinated. These two species show prominent and distinct morphological differences, and their taxonomic status is indisputable. *Howea forsteriana*, the kentia or thatch palm, is characterized by multiple spikes in each inflorescence and has straight leaves with drooping leaflets. *H. belmoreana*, the curly palm, bears a single spike in each inflorescence and has recurved leaves with ascending leaflets. There are many locations throughout Lord Howe Island in which the species occur sympatrically, yet putative hybrids are rarely reported; the extensive fieldwork of Savolainen *et al*. (2006a) identified only five specimens with intermediate morphologies.

The distributions of *H. forsteriana* and *H. belmoreana* are dependent on soil pH. *H. belmoreana* is found in neutral and acidic volcanic soils, while *H. forsteriana* more frequently inhabits calcarenite, a recent basic sedimentary formation found predominantly in the lower parts of the island. Despite these preferences, both species occur sympatrically in 11 of the 55 study quadrants that contain palms. Phenological data indicate that the species are reproductively isolated, with *H. forsteriana* flowering before *H. belmoreana*. The peak flowering period of *H. forsteriana* occurs approximately six weeks before that of *H. belmoreana*, and there is little overlap of peak flowering periods between the two species. *H. belmoreana* is synchronous, whereas *Howea forsteriana* is protandrous at the population level, with male flowering peaking two weeks before female receptivity. However, in the sampling site where *H. forsteriana* occurs on volcanic rather than calcareous substrates, asynchronous maturation is not observed; although substrate-induced physiological changes cannot explain the difference in flowering periods between the species.

Molecular data strongly support the monophyly of *Howea* and a sister relationship to the monotypic Australian genus *Laccospadix*. Using two different molecular-dating methods, Savolainen *et al*. (2006a) estimated the split between *Howea* and *Laccospadix* to be 4.57–5.53 million years old, and that the two *Howea* species diverged about 1.92 million years ago (based on a nonparametric rate-smoothing method) or just less than 1 million years ago (based on a Bayesian method), long after Lord Howe Island was formed.

The analysis of molecular variance (AMOVA, Excoffier *et al*. 1992; Excoffier 2001) based on 274 polymorphic amplified fragment length polymorphism (AFLP) loci shows that within-species genetic variation is low ($F_{SC} = 0.144$) and at the same time the species diverged significantly one from another ($F_{CT} = 0.626$). Genetic divergence within the genome follows an L-shaped distribution, with most loci showing low $F_{ST}$ and only four loci differing more strongly between the two species than expected under neutrality. These four loci were the only markers that were fixed in the two species.

On the basis of these data, Savolainen *et al*. (2006a) advance the following scenario. The ancestor of *Howea* reached Lord Howe Island, most likely from Australia, as long as 4.5–5.5 million years 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, which corresponds well to the age of the split between the two *Howea* species recovered from the molecular clocks. The absence of protandry in *H. forsteriana* on less basic soils suggests that the conspicuous flowering time difference may have arisen initially as a physiological response to a new substrate, thus introducing a bias in random mating

and kicking-off speciation. Because the island is so small, volcanic and calcarenite substrates are intermixed, both species co-occur in ~20% of their modern distribution range and both are wind-pollinated. Savolainen *et al.* (2006a) argue that it is very unlikely that the two species have ever been truly spatially isolated from each other, despite the strong divergence in edaphic preferences.

## Mathematical model

We will model the process of invasion by a specialist species into an environment where a new ecological niche is available (Kawata 2002; Gavrilets & Vose 2005; Gavrilets *et al.* 2007). Most modelling work on evolution in a spatially heterogeneous environment assumes *soft* selection (e.g. Kisdi & Geritz 1999; Spichtig & Kawecki 2004 and references therein; but see DeMeeus *et al.* 1993) and does not consider population densities explicitly. In contrast, selection for local adaptation in our model is both density-dependent and *hard* (*sensu* Christiansen 1975). That is, the contribution of each niche to offspring depends on the fitness of individuals in the niche. The following describes basic components of the model.

### Space and environment

In our model, space is represented by a rectangular array of 'cells' each of which can be empty or occupied by a single adult plant. Each cell is characterized by four environmental factors: three factors, $\theta_i$ ($i = 0,1,2$), are scaled to take any value from the interval [0, 1] and one factor, $e$, is given by an integer. Factors $\theta_0$, $\theta_1$, and $\theta_2$ control the effects of environment on survival to the seedling stage, survival to the adult stage, and fertility, respectively. Factor $e$ is interpreted as a number of weeks by which environment accelerates flowering. (We use the term 'week' but this can be substituted for any other appropriate interval of time.) We are interested in the case when there are only two types of environment. The upper half of the array of cells represents basalt soil (niche 0 with $\theta_0 = \theta_1 = \theta_2 = e = 0$) whereas the lower half of the array represents calcarenite soil (niche 1 with $\theta_0 = \theta_1 = \theta_2 = e = 1$, $e \geq 0$).

In models with $e = 0$, speciation, if observed, is sympatric. In models with $e > 0$, speciation, if observed, is parapatric (because plants that happen to grow on the same soil type mate more often since there is a greater similarity in their flowering periods).

### Individuals

Generations are discrete and nonoverlapping. Individuals are diploid and produce flowers of both male and female types. Each individual has a number of additive quantitative characters:

- three 'ecological characters' $x_i$ ($i = 0,1,2$) controlling survival to the seedling stage, survival to the adult stage, and fertility, respectively; these characters are scaled to take any value from the interval [0,1]; and
- two flowering time characters (given by integers): trait *a* controlling the 'week' of the commencement of flowering and trait *b* controlling the number of consecutive 'weeks' the plant is flowering.

All these characters are controlled by different diallelic loci with equal effects in an additive way. Mutations occur at equal rates across all loci; the probabilities of forward and backward mutations are equal.

There are also a number of unlinked neutral loci with a large number of alleles subject to stepwise mutation (Ohta & Kimura 1973). These loci have higher mutation rates and will be used to evaluate the levels of genetic divergence within and between species that one would observe if using microsatellite markers.

### Life cycle

The life cycle consists of: (i) random seed dispersal across a limited area around the plant; (ii) two-stage density-dependent viability selection (via differences in the probabilities of surviving to the seedling stage and to the adult stage); and (iii) random pollen dispersal, mating, and seed production (with account of fertility selection).

### Viability selection

Of all seeds arriving to the cell, no more than one develops into an adult plant. Let

$$v_i = \exp\left[-0.5\left(\frac{x_i - \theta_i}{\sigma_i}\right)^2\right],$$

where $\sigma_i > 0$ are constants controlling the strength of selection on ecological characters ($i = 0,1,2$). Note that smaller values of $\sigma_i$ mean stronger selection. We use a two-step selection procedure. At the first stage, each seed develops into a seedling with probability $v_0$. At the second stage, we choose a single adult plant out of all seedlings in the cell with the probabilities proportional to $v_0 v_1$. Note that the ecological trait $x_0$ contributes to the survival at both stages.

### Flowering period

The overall flowering period is subdivided into a number of nonoverlapping intervals ('weeks'). Each individual plant produces male and female flowers during weeks $a - e, a - e + 1, \ldots, a - e + b$, where $e$ is the effect of environment on the onset of flowering. The allelic effects at the loci controlling flowering period characters *a* and *b* are equal to

0 and 1, respectively. This implies that the range of possible trait values is between zero and twice the number of the corresponding loci.

### Pollen dispersal

During each week, each flowering plant can receive pollen from any other plant flowering during the same week, irrespective of the distance between the plants. Self-fertilization is not allowed.

### Fertility selection

Relative fertility of an individual with ecological traits $x_0$, $x_1$ and $x_2$ is given by the product $v_0v_1v_2$. The overall number of seeds and pollen produced by a plant is taken from Poisson distributions with parameters $K_s v_0 v_1 v_2$ and $K_p v_0 v_1 v_2$, where $K_s$ and $K_p$ control the maximum possible numbers of seeds and pollen, respectively. For each plant, each flowering week contributes approximately equally to the number of seeds and pollen. For example, for a plant with trait $b$, the number of seeds produced during a particular week is taken from a Poisson distribution with parameter $K_s v_0 v_1 v_2 / (b + 1)$.

We assume that $K_p$ is effectively infinite so that there is no pollen limitation and each seed is fertilized if there is at least a single other plant flowering during the corresponding week. The assumption of no pollen limitation implies that any costs of mate choice, which can easily prevent divergence and speciation (Bolnick 2004; Gavrilets 2004, 2005; Gourbiere 2004; Kirkpatrick & Nuismer 2004; Waxman & Gavrilets 2005a), are absent. (Here, the role of 'mate choice' is played by the 'choice' of the flowering period.)

Note that our description of selection at different stages implies that trait $x_0$ contributes to all three fitness components (survival to seedling, survival to adult, and fertility), trait $x_1$ contributes to two fitness components (survival to adult and fertility), and trait $x_2$ contributes only to fertility. These assumptions formalize an intuitively appealing idea that some of the individual's features that help at an earlier stage of the life cycle also contribute at later stages. Examples may include traits that allow a more efficient extraction of water or nutrients from a particular soil, or rapid growth on a particular soil. The existence of correlations between fitness-related phenotypic traits measured in plants of different ages has been established empirically (e.g. Lambeth 1980; Bovi & Godoy 1991; Hodge & White 1992).

For simplicity we assume that parameters $\sigma_i$ controlling the strength of natural selection are the same for all traits, i.e. $\sigma_i = \sigma$. Parameter $\sigma$ plays an important role in our simulations. Table 1 helps understand the biological meaning of the different numerical values for this parameter used in our simulations.

**Table 1** Fitness components of a specialist for one niche in the other niche and for a generalist in either niche for different values of $\sigma$: relative survival to the seedling stage $v_0$, relative survival to the adult stage $v_0v_1$, and relative fertility $v_0v_1v_2$. Larger values of $\sigma$ imply larger values of the fitness components and, thus, weaker selection for local adaptation. Fitness of a specialist in the niche it is adapted to is always one, irrespective of the value of $\sigma$

| | Specialist | | | Generalist | | |
|---|---|---|---|---|---|---|
| $\sigma$ | $v_0$ | $v_0v_1$ | $v_0v_1v_2$ | $v_0$ | $v_0v_1$ | $v_0v_1v_2$ |
| 0.75 | 0.41 | 0.17 | 0.07 | 0.8 | 0.64 | 0.51 |
| 0.85 | 0.5 | 0.25 | 0.13 | 0.84 | 0.71 | 0.6 |
| 0.95 | 0.58 | 0.33 | 0.19 | 0.87 | 0.76 | 0.66 |
| 1.15 | 0.69 | 0.47 | 0.32 | 0.91 | 0.83 | 0.75 |
| 1.35 | 0.76 | 0.58 | 0.44 | 0.93 | 0.87 | 0.81 |
| 1.75 | 0.85 | 0.72 | 0.61 | 0.96 | 0.92 | 0.88 |

### Seed dispersal

With probability $d$, each seed is dispersed in a random direction at distance $1 < l < l_{max}$ taken from a truncated normal distribution

$$\Pr(l) = \exp\left[-0.5\frac{l^2}{\sigma_p^2}\right],$$

where $\sigma_p$ is a characteristic distance of seed dispersal and $l_{max}$ is the maximum dispersal distance. With probability $1 - d$, each seed stays in the 'cell' of origin.

### Initial conditions

The founding population is represented by a small number of individuals (seeds) that are perfectly adapted (i.e. all $x_i = 0$) for the basalt soil niche (i.e. $\theta_i = 0$). The flowering time characters of the founders are set exactly at the middle of the range of possible values so that $a$ and $b$ are equal to the number of the corresponding loci. All individuals are homozygous so that no genetic variation is present. These assumptions imply that among the founders, all individual plants flower during exactly the same time interval starting at week $a$ and ending at week $a + b$. Each microsatellite locus was heterozygous with two intermediate alleles out of $2^8$ possible alleles.

### Parameters

To analyze our model, we used individual-based simulations, which we ran for 50 000 generations, roughly corresponding to 500 000 years (assuming that palms start flowering in about 10 years). Population-level data were saved every 100th generation; individual-level data were saved every 5000th generation. The results below are based on 20 runs for each parameter combination. The following summarizes

parameters that did not change: system size $32 \times 128$ cells, mutation rate $10^{-5}$ per generation for loci controlling traits $x_0$, $x_1$, $x_2$, $a$ and $b$, mutation rate $10^{-3}$ per generation for 'microsatellites', average number of seeds per plant $b = 16$, the probability of seed dispersal $d = 0.3$, the maximum seed-dispersal distance $l_{max} = 3$, and the characteristic distance of seed dispersal $\sigma_p = 1$. Although we wished to produce not only qualitative but quantitative results, in the absence of precise data, numerical values for $b$, $d$, $l_{max}$ and $\sigma_p$ were chosen on the basis of intuition and for computational convenience. The number of 'microsatellites' was eight. All loci were unlinked. For simplicity the number of loci per traits $x_0$, $x_1$, $x_2$, $a$ and $b$ was the same. This number is denoted as $L$ below.

The reader might be curious why the maximum population size in our simulation ($4096 = 128 \times 32$ adults) is much smaller than we have been able to use previously (Gavrilets & Vose 2005 and the accompanying paper). In our model, each adult plant can flower for a number of periods (up to 65 in our simulations) and is effectively considered as an independent entity multiple times. Therefore, from the computational point of view, the 'effective' population size is much larger than 4096.

The model was implemented in C. The code is available upon request.

## Theoretical results

In our simulations, we have observed three different dynamic regimes: (i) a failure to colonize the new niche; (ii) the evolution of a single generalist species utilizing both niches relatively inefficiently; and (iii) the emergence of a new species specialized to the new niche, which occurs simultaneously with strong divergence in flowering period characters between the species. In describing these regimes below we will focus on the distribution of individuals across space, levels of local adaptation and the distribution of flowering period characteristics. The level of local adaptation will be measured by the 'overall matching', which we define as the average (across all three ecological characters) reduction in fitness relative to the maximum possible fitness.

In the first regime (illustrated in Fig. 1), only a small number of members of the original species grow in the parts of niche 1 (calcarenite soil) bordering niche 0 (basalt soil). These plants have very low fitness in their environment (see the first three columns in Table 1). Very low levels of genetic variation in ecological traits are maintained by a balance of mutation and selection. The flowering period characters evolve largely in a neutral fashion. Low levels of genetic variation in flowering period traits are maintained by a balance of mutation and random drift.

In the second regime (illustrated in Fig. 2), a new generalist species evolves and spreads through the whole system. This species has a relatively low fitness on both soil
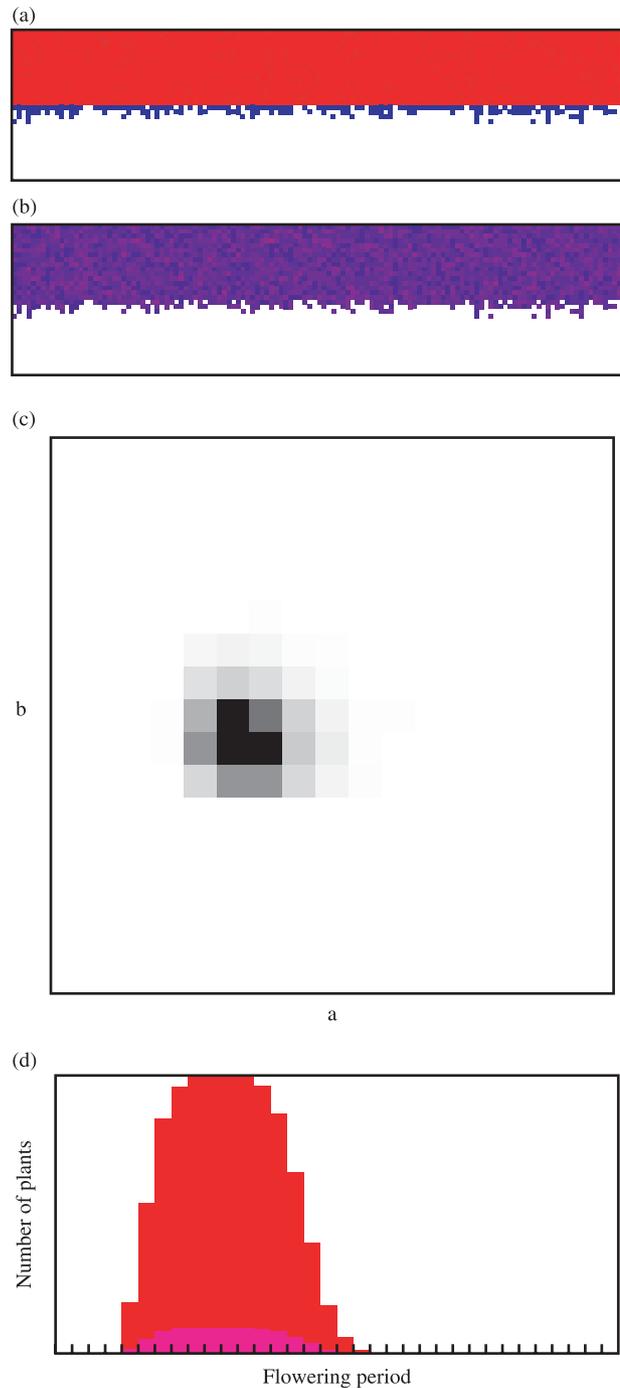


**Fig. 1** No invasion. (a) The 'overall matching' of each plant with its environment colour-coded from red (high) to blue (low). Empty cells are uncoloured. (b) The onset of flowering trait $a$ colour-coded from red (late) to blue (early). (c) The distributions of the flowering period traits $a$ and $b$ in the whole population with darker areas corresponding to more frequent combinations of traits. (d) The histograms showing the number of plants flowering during each week in niche 0 (basalt soil, red colour) and niche 1 (calcarenite soil, blue colour). The purple colour is given where red colour overlaps with blue colour. Shown is run 0 with $\sigma = 0.75$, $e = 0$ and $L = 8$.

(a)



(b)



(c)

b

a

(d)

number of plants

Flowering period
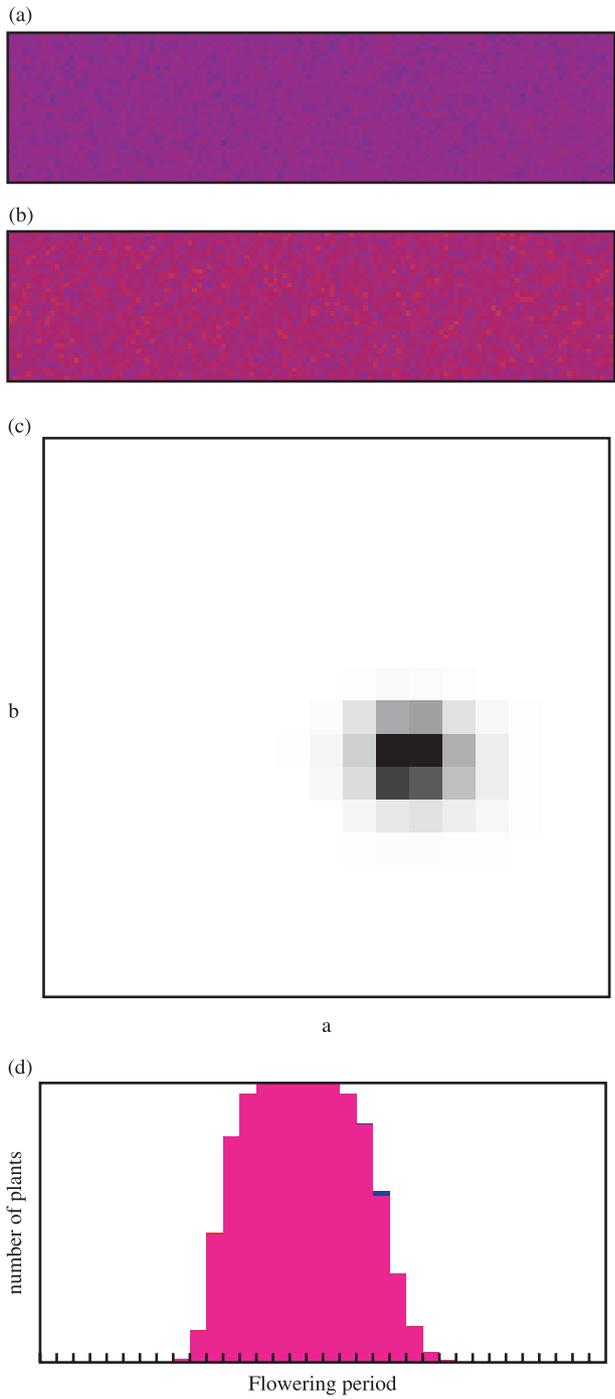
**Fig. 2** Evolution of a generalist species. See the legend of Fig. 1. Shown is run 0 with $\sigma = 0.95$, $e = 0$ and $L = 8$.

(a)



(b)



(c)

b

a

(d)

number of plants

Flowering period

**Fig. 3** Speciation. See the legend of Fig. 1. Shown is run 4 with $\sigma = 0.95$, $e = 2$ and $L = 8$. In part (d), the distribution of flowering in niche 1 is shifted right by $e = 2$ units to more clearly illustrate the genetic effects on the divergence in flowering periods.

types (compare the colour of Fig. 2(a) with that of 1(a); also see the last three columns in Table 1). Relatively large levels of genetic variation in the ecological characters can be maintained by a balance of selection and migration, and some divergence between the populations in the two niches can be observed. Somewhat larger genetic variation

(relative to the case of no invasion) can be maintained in the flowering period traits.

In the third regime (illustrated in Fig. 3) a new species evolves on the calcarenite soil (niche 1). The two species are very well adapted to their own niches, the distribution of

traits a and b becomes bimodal, and the flowering periods strongly diverge so that very little overlap of flowering periods is present.

Different regimes were identified largely unambiguously by visual inspection of graphs similar to those presented in Figs (1–3). Table 2 shows how the frequencies of different outcomes depend on the strength of natural selection, $\sigma$; on the effect of the environment in niche 1 on the onset of flowering, $e$; and on the number of loci underlying the traits, $L$. When $e = 0$, speciation, if observed, is sympatric.

**Table 2** Number of times the population has not colonized the new habitat (No Inv), a generalist species evolved (Generalist), or speciation occurred (Speciation) for different parameter combinations. Also shown is the average time to invasion (ATI) and the average time to speciation (ATS) over runs in which these events were observed. The last column shows the average rate of hybridization $h$ (in percentage) in the last generation over the runs resulting in speciation. Only the sets with at least eight speciation runs were used for computing $h$. Parameters $\sigma$ measures the strength of natural selection, $e$ is the effect of the environment in niche 1 on the onset of flowering, and $L$ is the number of loci underlying each trait. When $e = 0$, speciation, if observed, is sympatric. When $e > 0$, speciation, if observed, is parapatric. 20 runs for each parameter combination (two runs are missing because of a computer crash). Note that since the data were collected only every 100th generation, any time to invasion below 100 was recorded as 100

| $\sigma$ | $e$ | $L$ | No Inv | Generalist | Speciation | ATI | ATS | $h$ |
|---|---|---|---|---|---|---|---|---|
| 0.75 | 0 | 4 | 20 | — | — | — | — | |
| | | 8 | 20 | — | — | — | — | |
| | | 16 | 20 | — | — | — | — | |
| | 2 | 4 | 20 | — | — | — | — | |
| | | 8 | 20 | — | — | — | — | |
| | | 16 | 20 | — | — | — | — | |
| | 4 | 4 | 1 | — | 19 | 3 979 | 3 768 | 0.02 |
| | | 8 | 20 | — | — | — | — | |
| | | 16 | 20 | — | — | — | — | |
| 0.85 | 0 | 4 | — | 1 | 19 | 465 | 15 532 | 0.05 |
| | | 8 | — | 12 | 8 | 535 | 31 400 | 0.09 |
| | | 16 | — | 20 | — | 794 | — | |
| | 2 | 4 | — | — | 20 | 259 | 600 | 0.04 |
| | | 8 | — | — | 20 | 482 | 5505 | 0.05 |
| | | 16 | — | 20 | — | 688 | — | |
| | 4 | 4 | — | — | 20 | 171 | 305 | 0.03 |
| | | 8 | — | — | 20 | 400 | 1 830 | 0.05 |
| | | 16 | — | 18 | 2 | 776 | 33 650 | |
| 0.95 | 0 | 4 | — | 3 | 17 | 106 | 15 500 | 0.08 |
| | | 8 | — | 12 | 8 | 106 | 35 075 | 0.19 |
| | | 16 | — | 20 | — | 100 | — | |
| | 2 | 4 | — | — | 20 | 100 | 755 | 0.06 |
| | | 8 | — | 4 | 16 | 100 | 8 875 | 0.1 |
| | | 16 | — | 17 | 2 | 106 | 31 400 | |
| | 4 | 4 | — | — | 20 | 100 | 330 | 0.04 |
| | | 8 | — | — | 20 | 100 | 2 625 | 0.06 |
| | | 16 | — | 17 | 2 | 100 | 22 550 | |
| 1.35 | 0 | 4 | — | 9 | 11 | 100 | 26 218 | 0.5 |
| | | 8 | — | 19 | 1 | 100 | 13 500 | |
| | | 16 | — | 19 | 1 | 100 | 49 500 | |
| | 2 | 4 | — | — | 20 | 100 | 2 740 | 0.22 |
| | | 8 | — | 10 | 10 | 100 | 24 940 | 0.27 |
| | | 16 | — | 20 | — | 100 | — | |
| | 4 | 4 | — | — | 20 | 100 | 970 | 0.24 |
| | | 8 | — | — | 20 | 100 | 10 930 | 0.22 |
| | | 16 | — | 18 | 2 | 100 | 37 000 | |
| 1.75 | 0 | 4 | — | 9 | 10 | 100 | 24 480 | 1.19 |
| | | 8 | — | 18 | 2 | 100 | 43 350 | |
| | | 16 | — | 19 | 1 | 100 | 43 700 | |
| | 2 | 4 | — | — | 20 | 100 | 10 335 | 0.42 |
| | | 8 | — | 15 | 5 | 100 | 37 540 | |
| | | 16 | — | 20 | — | 100 | — | |
| | 4 | 4 | — | — | 20 | 100 | 4 560 | 0.33 |
| | | 8 | — | 6 | 14 | 100 | 25 586 | 0.6 |
| | | 16 | — | 18 | 2 | 100 | 41 650 | |

When $e > 0$, speciation, if observed, is parapatric. We notice that if selection for local adaptation is too strong (i.e. $\sigma = 0.75$) then the new ecological niche remains empty. As the strength of selection decreases, then the frequency at which a generalist species evolves increases. Speciation is the easiest to achieve if the number of loci underlying the traits is relatively small (i.e. $L = 4$). When the number of loci is relatively large (i.e. $L = 16$) the most common outcome is the evolution of a generalist species. Speciation can be observed even if the environment does not directly affect the time of the onset of flowering (i.e. if $e = 0$). However, relatively small positive values of $e$ (comparable in magnitude to the effects of a single locus substitution) dramatically increase the probability of speciation, making it almost guaranteed under certain configurations of parameters. Overall, the most conducive conditions for speciation are intermediate strength of selection, small number of loci and the presence of direct environmental effect on the onset of flowering. The graphs similar to those given in Figs 1–3 corresponding to all runs summarized in Table 2 can be viewed at http://www.tiem.utk.edu/~gavrila.

Table 2 also shows the average time to invasion and the average time to speciation over runs in which these events were observed. The time to invasion was defined as the time until the number of adult individuals in niche 1 reached 95% of the maximum possible number. One can see that if invasion of the new niche is to happen, in most cases it occurs very fast. The time to speciation was defined as the time until the average value of trait $x_0$ in the population in niche 1 reached 0.9 for the first time. The overall effects of the parameters on the average time to speciation are similar to those on the probability of speciation. That is, the average time to speciation decreases with decreasing the number of loci $L$ and increasing the environmental effect $e$. Small and large values of parameter $\sigma$ (characterizing the strength of selection for local adaptation) increase the average waiting time to speciation.

The last column in Table 2 presents the average value of a hybridization index $h$ in the last generation of runs resulting in speciation. Index $h$ was defined as the proportion of seeds produced as a result of mating across the boundary between the two niches. The hybridization index $h$ is very small (on the order of one over several thousand) if selection for local adaptation is at least moderately strong and increases to over one percent for the weakest selection considered ($\sigma = 1.75$). Index $h$ increases with the number of loci $L$ and decreases with environmental effect on flowering $e$.

The nature of a state with a single generalist species requires some clarification. In fact, we observed qualitatively different situations (cf. Spichtig & Kawecki 2004; Gavrilets et al. 2007). If selection for local adaptation is relatively weak (e.g. $\sigma = 1.35$), the generalist species is almost monomorphic with a very low level of genetic variation maintained in each ecological trait. Half of the corresponding loci are almost fixed for allele 0, while the rest are almost fixed for allele 1. There is no genetic divergence in the ecological trait loci between the subpopulations inhabiting the two niches. If selection is strong (e.g. $\sigma = 0.85$) and the number of loci is small (e.g. $L = 4$), the generalist species maintains very high levels of genetic variation with allele frequencies in the loci controlling the ecological traits $x_0$ and $x_1$ close to 0.5. There is also some genetic divergence between the subpopulations in the two niches in these two traits. For intermediate cases (e.g. with $\sigma = 0.95$ or with $\sigma = 0.85$ but with $L = 8$ or 16), variation and divergence are maintained only in trait $x_0$. The differences in the effects of parameters $\sigma$ and $L$ on different traits are explained by the fact that trait $x_0$ experiences the strongest disruptive selection (because it contributes to all three fitness components), whereas trait $x_2$ experiences the weakest disruptive selection (because it only contributes to fertility).

When speciation occurs, the system usually goes through a generalist stage. This implies that specialists for the first niche are lost temporarily and then recreated again when the generalist species splits into two specialist species. Speciation via a generalist state did not happen, except with $\sigma = 0.75$ (very strong selection), and $L = 4$ and $e = 4$. Note that in this case few mutations might be sufficient to produce the specialist for the empty niche. The new specialist will immediately be strongly diverged from the ancestral population in terms of flowering period because of the large environmental effect on the onset of flowering.

Whenever speciation occurs, one species almost always evolves to a state with values of $a$ and $b$ close to zero, i.e. with the earliest possible onset and shortest possible duration of flowering. This species is characterized by a very small level of genetic variation. The other species has a relatively broad flowering period and a relatively large level of genetic variation. If an environmental effect on the onset of flowering is present (i.e. if $e > 0$), it is the derived species that flowers earlier and has smaller genetic variation.

If speciation occurs then one observes a very small overlap in flowering periods between the species, which implies very strong reproductive isolation. In our simulation the latter was characterized in two ways. As we have discussed above, we computed a simple hybridization index $h$ equal to the proportion of flowers in one niche fertilized by pollen from another niche (see the last column in Table 2). The hybridization index is typically very low. Second, we looked at the levels of within- and between-species divergence at neutral 'microsatellite' loci, using the data collected every 5000th generation. Specifically, we calculated statistics $R_{ST}$ (the ratio of the genetic variance among groups and the total genetic variance) and $R_{IS}$ (the ratio of the genetic variance among individuals within groups and the total genetic variance) using *micsatfs* (R. E. Strauss, unpublished; publicly available at http://www.biol.ttu.edu/Strauss/Matlab/matlab.htm). To compute these values,

we pulled adult individuals into two groups according to the soil type. Some results are shown in Fig. 4. This figure shows that in runs resulting in speciation, $R_{ST}$ values increase rapidly once speciation is initiated. In contrast, $R_{IS}$ values remain low in all runs. These observations and numerical values observed are compatible with the levels of genetic divergence between and within species estimated by Savolainen *et al.* (2006a). Note that in runs that did not result in speciation, $R_{ST}$ values remain at levels similar to those observed in Fig. 4 before the onset of rapid divergence.

## Discussion

Overall, our results show that relatively rapid (< 50 000 generations) colonization of a new ecological niche and speciation via local adaptation and divergence in flowering



**Fig. 4** The dynamics of $R_{ST}$ (solid line) and $R_{IS}$ (dashed line). (a) The five runs that resulted in speciation with σ = 0.85 (relatively strong selection), $L = 8$ and $e = 0$. (b) The nine runs that resulted in speciation with σ = 1.35 (relatively weak selection), $L = 8$ and $e = 2$.

period are theoretically plausible if: (i) the number of loci underlying the traits is small; (ii) the strength of selection for local adaptation is intermediate; and (iii) an acceleration of flowering by a direct environmental effect associated with the new ecological niche is present.

The observation that rapid nonallopatric speciation is very unlikely unless the number of loci underlying the traits involved in local adaptation and reproductive isolation is small has been made repeatedly previously (e.g. Gavrilets 2004; Gavrilets & Vose 2005; Gavrilets *et al.* 2007). The reason for this observation is simple. In the presence of gene flow between the diverging groups disruptive selection must be strong and the advantages of evolving reproductive isolation must be significant. Smaller number of loci imply larger locus effects, stronger selection on each individual locus and, simultaneously, weaker effects of recombination, which destroys coadapted gene complexes (and linkage disequilibrium between the loci). All this promotes nonallopatric speciation. As reviewed by Macnair (1993), the number of plant taxa endemic to particular (e.g. serpentine) soils is relatively large, and the ability of plants to tolerate the toxic metal present does indeed appear to often be controlled by one or a small number of genes. This is compatible with our observations. Reversing our argument one can claim that genetics of traits underlying rapid and extensive diversification and speciation in the presence of gene flow must be simple (Gavrilets & Vose 2005), at least in the sense that the number of loci is small. This is a testable prediction.

Rapid evolution of two reproductively-isolated specialist species requires intermediate strength of selection for local adaptation. When selection is weak, then a generalist has relatively high fitness in both habitats, favouring evolution of a single generalist species. When selection is very strong, an ancestral specialist species maintains relatively low genetic variation which prevents (or at least significantly delays) the emergence of new genotypes that may survive in the new niche and seed a new species there. It is only with intermediate strength of selection that enough of genetic variation is preserved in the ancestral specialist species, so that a generalist species evolves but then specialization is favoured because it increases fitness (e.g. Kisdi & Geritz 1999; Spichtig & Kawecki 2004). Evolution of two specialists proceeds simultaneously with the divergence in flowering times as this prevents the deleterious gene flow and increases overall adaptation.

We have only considered the case of additive characters. In principle, particular genetic architectures may accelerate speciation. For example, if alleles are dominant in the environment where they are advantageous, and recessive in the environment where they are deleterious, speciation will be easier to accomplish. Similarly, some forms of epistasis that promote the accumulation of high levels of genetic variation within the ancestral niche will simplify
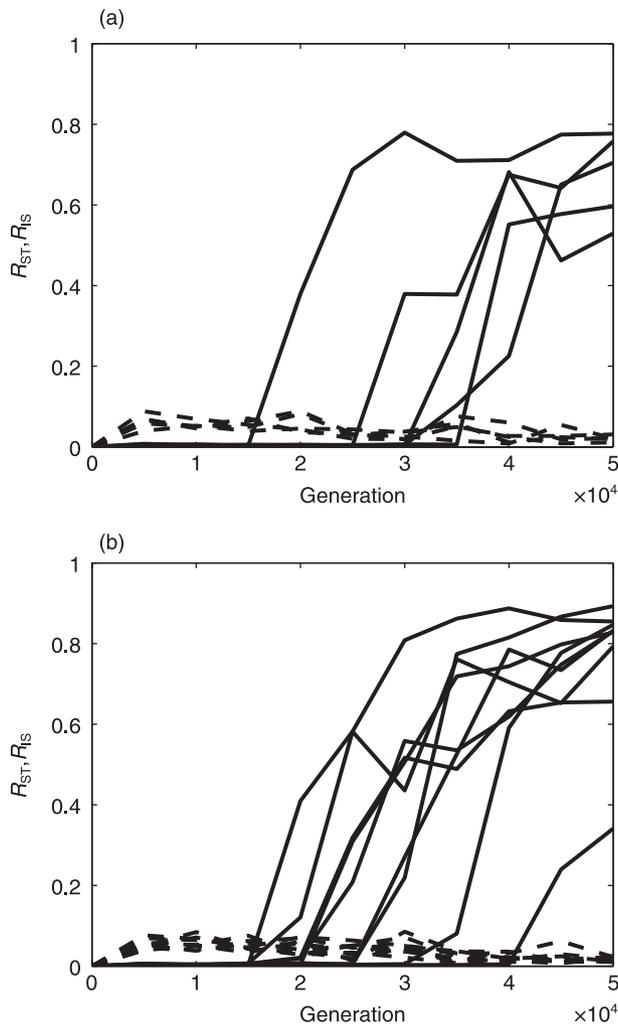
conditions for the invasion of a new niche. We are not aware of data supporting the plausibility and generality of such genetic architectures though. We assumed that some traits affected more than one fitness component. Assuming that each trait controls an independent fitness component is not expected to affect our results.

Environmental acceleration of flowering via the effects, for example, of soil moisture, temperature or pH on plant physiology is common (e.g. Vasek & Sauer 1971; Macnair & Gardner 1998; Silvertown *et al.* 2005). Such effects represent a form of phenotypic plasticity (Pigliucci 2001). If environment accelerates flowering in one niche relative to another, then significant reproductive isolation can evolve even without any differences in selection between the niches (Stam 1983). This happens because of a differential gene flow, with genes for early flowering being preferentially transported with pollen to the niche that induces early flowering, and genes for late flowering being preferentially transported to the niche that induces late flowering (Stam 1983). Adding differential selection for local adaptation dramatically increases the extent of resulting genetic divergence in flowering periods (Stam 1983 and our results above). As noticed by an anonymous reviewer, no concrete evidence seems to exist that the morphological differences between the two species described by Savolainen *et al.* (2006a) are related to the adaptation to different conditions in the respective niches. These differences could have evolved by other factors, e.g. random genetic drift, after reproductive isolation has been achieved, via the Stam effect.

If environment directly alters the flowering period then speciation can no longer be called sympatric, at least if one uses the strict definition of Gavrilets (2003, 2004). The reason is that in this case, plants that happen to grow on the same soil type mate more often because there is a greater similarity in their flowering periods. Speciation in this case should be called parapatric. Therefore, strictly speaking the data and arguments of Savolainen *et al.* (2006a) provide support for parapatric rather than for sympatric speciation of *Howea* palms on Lord Howe Island. The Lord Howe Island is rapidly eroding and its size at the presumed time of speciation (0.5–1.9 million years ago) was much larger than at present (Stuessy 2006). This implies that there could have been opportunities for spatial isolation between diverging species that are not there anymore (Stuessy 2006). As noticed by an anonymous reviewer, Ball's Pyramid, the tiny landmass 23 km southeast of the island, was probably much larger in size in the past and therefore offered the possibility of allopatric speciation. Savolainen *et al.* (2006b) consider this unlikely though. In any case, our results clearly show that rapid speciation can also occur if the environmental effect of the onset of flowering is absent (i.e. if $e = 0$). In this case, speciation is sympatric even according to our strict definition.

Our conclusions, however, should not be interpreted as the statement that sympatric or ecological speciation occurs easily in this model because a number of assumptions and conditions (highlighted in our paper) have to be satisfied. As is apparent in this and many other models, genetics strongly constrains the dynamics of ecological speciation. As we discussed in detail previously on a number of occasions (e.g. Gavrilets 2004, 2005, Waxman & Gavrilets 2005a, b), we view the occasionally made claims that sympatric speciation occurs easily (e.g. Dieckmann & Doebeli 1999; Higashi *et al.* 1999; Kondrashov & Kondrashov 1999; Doebeli 2005; Doebeli & Dieckmann 2005) as unjustified.

The degree of reproductive isolation observed in our simulations (as shown by the flowering period overlaps, by the percentage of hybrids, and by the divergence in neutral markers) is very strong. This observation, as well as similar observations made previously in related mathematical models (Crosby 1970; Stam 1983; van Dijk & Bijlsma 1994), suggest that divergence in flowering period represents a very efficient way of achieving strong premating isolation. Sometimes early flowering can be adaptive by itself, e.g. if it allows plants to produce seeds before drought-induced death (Macnair & Gardner 1998). In this case, the onset of flowering can be viewed as a 'magic trait' (Gavrilets 2004), which simultaneously controls both local adaptation and reproductive isolation. 'Magic traits' greatly simplify nonallopatric speciation (Gavrilets 2004, 2005). Divergence in flowering period is an example of temporal (allochronic) isolation (reviewed in Coyne & Orr 2004, pp. 202–210). Mayr (1963, pp. 474–476) was very skeptical about the possibility of achieving strong reproductive isolation via allochronic isolation. However, our results and those of related theoretical studies suggest that the evolution of allochronic isolation can be a very efficient mechanism for speciation in general.

Existing data show that divergence in flowering period resulting in substantial reproductive isolation between neighbouring populations can be very rapid (e.g. McNeily & Antonovics 1968; Antonovics & Bradshow 1970; Davies & Snaydon 1976; Snaydon & Davies 1976; Silvertown *et al.* 2005). Hendry *et al.* (2007) argue that significant progress towards ecological speciation can be achieved on the timescale of a few dozen generations. In our model, under the most favourable conditions the timescale of ecological speciation is on the order of several hundred to several thousand generations. Achieving the speed of ecological speciation envisioned by Hendry *et al.* (2007) would require very substantial levels of initial genetic variation besides other conditions, discussed in detail above.

The duration of transition from the state with one species to two species was very short — a few hundred to a few thousand generations. This is another general feature of models of nonallopatric speciation (Gavrilets 2004) which is compatible with patterns of 'punctuated equilibrium'

(Eldredge 1971; Eldredge & Gould 1972; Gould & Eldredge 1993; Gould 2002; Eldredge *et al*. 2005).

In our simulations, whenever speciation occurs one species almost always evolves to a state with the earliest possible onset and shortest possible duration of flowering. This species is also characterized by a very small level of genetic variation. The other species has a relatively broad flowering period and a relatively large level of genetic variation. If an environmental effect on the onset of flowering is present, it is the derived species that flowers earlier and has smaller genetic variation. These theoretical features of the flowering period distribution and genetic variation can be tested against data.

As with most other complex numerical models, ours has a number of potentially important limitations and does not allow complete investigation of the parameter space. Here we discuss expected effects of changing some parameters and assumptions of our model. To achieve computational efficiency, we assumed nonoverlapping generations. Intuition suggests that allowing for overlapping generations will decrease the efficiency of selection (because low-fitness individuals will be able to contribute to offspring) and make speciation more difficult. For simplicity we assumed that environmental effect on flowering period is present for both sexes while in *Howea* this effect is apparently present only for male flowers. Restricting the environmental effect to one sex only should make speciation more difficult. We neglected random microenvironmental effects on both ecological and flowering period characters. With regard to ecological traits, these effects are expected to decrease the efficiency of natural selection (e.g. Bürger 2000), making speciation more difficult. A similar effect is expected if one includes random microenvironmental effects on the flowering period traits because these effects will broaden flowering periods resulting in more gene flow between the diverging groups. The population sizes we managed to handle computationally are much smaller than those for the *Howea* species on the Lord Howe Island. However, increasing the population sizes is expected to make speciation easier as it will increase both the efficiency of selection and the number of beneficial mutations. We neglected any costs of choosiness assuming infinite supply of pollen. (Here, plant choosiness concerns the 'choice' of the flowering period.) Previously, van Dijk & Bijlsma (1994) explicitly studied the effects of pollen limitation on the probability of speciation and observed that even small costs of choosiness dramatically reduced the probability of speciation. We expect the same effect in our model (see also Gavrilets 2004). In fact, we can speculate that costs of 'choosiness' in palms should be very low because otherwise rapid speciation would be very difficult to achieve.

Although useful information on *Howea* palms on the Lord Howe Island exists now, theoretical research would definitely benefit from additional data. In particular, it is important to have precise and direct information on the effect of soil characteristics on the flowering periods, on the strength of selection for local adaptation (acting via viability, survival to the seedling stage and fertility differences) and on the patterns of pollen and seed dispersal. Of equal importance would be to know the spatial distributions of different soil types and different plants across the island. Finally, the knowledge of the number of genes involved in ecological and flowering period traits, their mutation rates, and linkage relationship would greatly help in obtaining more precise theoretical conclusions about the plausibility of different scenarios of speciation of palms on the Lord Howe Island.

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