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Aspects of biosubsistence in *Sirindhornia* (Orchidaceae): are the narrow endemics more reproductively restricted than their widespread relative?

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Narrowly (neo)endemic species often attract special attention in conservation contexts, because their restricted distributions render them more vulnerable than most widespread species. However, little attention is given to the question whether time since speciation is the (only) factor responsible for the narrow ranges of neoendemics, or if biological or ecological factors are (also) involved. The Southeast Asian orchid genus *Sirindhornia* comprises three terrestrial species. In Thailand, we compared demographic and reproductive characteristics between the local endemics *S. mirabilis* and *S. pulchella* and the widespread *S. monophylla*. The three species had similar demographic characteristics, but different reproductive attributes. In most contexts where they differed, the local endemics were more reproductively restricted than the widespread *S. monophylla*. Thus, the latter exhibited higher relative fruit set, higher seed production per inflorescence and more equal individual contributions of progeny. However, recruitment appeared to be more efficient in *S. pulchella* than in the other two species.

Key words: conservation, demography, endemism, orchids, pollination, recruitment

Introduction

The orchid family is rich in narrow endemics — taxa being restricted to single mountains, islands or other narrowly delimited topographical units. Narrowly endemic orchids are universally perceived as neoendemics in the sense of Stott (1981): "Neoendemics, which are also variously called autochthonous, progressive or secondary endemics, represent 'new' taxa which have arisen by differential evolution in a particular area from which they have not yet spread or

are unable to spread". Results from studies of specific cases consistently support this view in genera such as *Dactylorhiza* (e.g. Hedrén 2001, Pedersen 2004, 2006), *Dendrochilum* (e.g. Pedersen 1997, Barkman & Simpson 2001, Wood 2001), *Epipactis* (e.g. Pedersen & Ehlers 2000, Squirrell *et al*. 2002) and *Gymnadenia s. lato* (e.g. Hedrén *et al*. 2000).

Narrowly (neo)endemic species often attract special attention in conservation contexts, because their restricted distributions obviously render them more vulnerable than most widespread species to threats such as collecting and habitat degradation. However, surprisingly little attention is given to the question whether time since speciation is the (only) factor responsible for the narrow ranges of neoendemics, or if biological or ecological factors are (also) involved. The term biosubsistence, in the sense of Hagemann (1996), encompasses a broad spectrum of biological notions such as demography, survival capability, seed dormancy and viability, growth forms, flower biology, seed dispersal, ecological requirements, diseases, etc. — all of which, in conjunction with environmental parameters, are potentially important for governing geographic range boundaries (Münzbergová & Herben 2005, Geber 2008). Aspects of biosubsistence might in some cases be at least as important as the time factor in explaining the narrow ranges of neoendemics, namely if these aspects put stronger restrictions on the neoendemics than on their widespread relatives. Insight in this field is important in relation to conservation, because range restrictions caused by aspects of biosubsistence would make the neoendemics even more susceptible to habitat degradation and other threats (Oostermeijer 2003) than if time since speciation was the only limiting factor. In this paper, we report our findings from a case study comparing limitations on sexual reproduction between two narrow endemics and a widespread species, all of which are assumed to be closely related.

Sirindhornia belongs to subtribe Orchidinae and comprises three species: *S. monophylla*, *S. mirabilis* and *S. pulchella* (Pedersen *et al*. 2002). *Sirindhornia monophylla* is widespread, being distributed from the province of Tak in northwestern Thailand across the Shan State of Myanmar to the southern Chinese province of Yunnan, whereas the two other species appear endemic to single limestone mountains in northern Thailand. *Sirindhornia mirabilis* is only known from the upper reaches of Doi Hua Mot (800–1100 m alt.) in Umphang Wildlife Sanctuary, province of Tak, which also accommodate the only known Thai occurrence of *S. monophylla*. The population of *S. mirabilis* (consisting of two subpopulations ca. 4 km apart) is restricted to an area measuring less than 10 km^2. A census of plants visible above ground in 2008 (K. Srimuang unpubl. data) revealed 791 individuals of *S. mirabilis* (and 284 of *S. monophylla*). *Sirindhornia pulchella* is only known from the upper reaches of Doi Chiang Dao (1800–2100 m alt.) in Chiang Dao Wildlife Sanctuary, province of Chiang Mai. The population (consisting of two subpopulations ca. 4 km apart) is restricted to an area measuring less than 10 km^2. A census of plants visible above ground in 2006 revealed 954 individuals (K. Srimuang unpubl. data).

To assess interspecific patterns of restrictions on sexual reproduction in *Sirindhornia*, we compare the magnitudes of relative fruit set, seed production per inflorescence, efficiency of recruitment and equality in individual female and male contributions of progeny. Furthermore, a rough demographic characteristic of each study population is provided to assertain the relevancy of comparing the reproductive parameters directly between the species.

It should be noted that Srimuang *et al*. (2010) utilized a minor share of the same data set (i.e. data on overall relative fruit set and pollinarium removal) as partial basis for interpreting reproductive success in relation to floral display.

Material and methods

Study species

All *Sirindhornia* species are geophytes with (supposedly root/stem) tuberoids, and all organs are renewed annually. During the adverse dry season, from September until March, the *Sirindhornia* plant survives underground, but during the rainy season it produces one (rarely two) leaves and sometimes an inflorescence with

mainly white to purple flowers that exude nectar in a distinct spur. All three species are genetically self-compatible and depend on insects, probably bees, for pollination (Srimuang *et al*. 2010). Like in other genera of tribe Orchideae, the pollen grains in *Sirindhornia* are firmly aggregated into a high number of massulae that in turn are fairly loosely assembled to form pollinia. The fruit is a capsule that produces numerous dust seeds and dehisces by longitudinal slits.

Study sites and plots

We studied *Sirindhornia mirabilis* and *S. monophylla* on Doi Hua Mot (Umphang Wildlife Sanctuary). This site consists of limestone cliffs, scrub forest and grassy slopes in the deciduous forest zone (800–1000 m alt.). *Sirindhornia mirabilis* primarily grows on limestone cliffs, whereas *S. monophylla* mainly occurs on open grassy slopes and in scrub forest with the canopy reaching 10 m or less. Dominant to frequent trees include *Wendlandia* sp., *Quercus* sp. and *Shorea siamensis*.

We studied *Sirindhornia pulchella* in the southwestern part of Doi Chiang Dao (i.e. on the ridge called Doi Luang, Chiang Dao Wildlife Sanctuary). This site consists of exposed limestone cliffs in the upper montane scrub zone (1800–2225 m alt.). Frequent plants include the palm *Trachycarpus oreophilus* and the large shrub *Rhododendron ludwigianum*.

Plots measuring 50 × 50 m were demarcated for studying each species in detail. Due to the particularly scattered occurrence of *S. monophylla*, we included three different plots for this species (but for the sake of convenience, they are referred to as one plot below).

Morphological size correlations and population structure

All *Sirindhornia* individuals that were visible above ground in the study plots were counted in 2006 (*S. mirabilis*, *S. monophylla*) or 2007 (*S. pulchella*). In all detected individuals of *S. mirabilis* (n = 105), *S. monophylla* (n = 120), and *S. pulchella* (n = 274), we measured the length of the longest leaf and the length (from apex to lowermost flower node) of the inflorescence (if any), and we counted the number of flowers in each inflorescence. Using the program SPSS for Windows 16, we calculated Pearson's correlation coefficient to test for correlations between leaf length on the one hand and inflorescence length and number of flowers per inflorescence on the other.

For the purpose of describing population structure in the plots for *S. mirabilis*, *S. monophylla* (both 2006) and *S. pulchella* (2007), we used the length of the longest leaf as a general indicator of plant size — as supported by the positive correlations that we found between leaf length and inflorescence length (in all three species) and between leaf length and number of flowers per inflorescence (in *S. mirabilis* and *S. monophylla* only), *see* below. Assuming a positive correlation between the size and age of individuals within each species, we referred all individuals to arbitrarily defined species-specific size classes (Table 1) to reveal the current demographic structure of each population sample. In order to assess the proportion of flowering individuals in each size class, we classified every individual as vegetative or flowering.

Flowering, reproductive success and pollinarium movements

The number of flowering individuals and the number of flowers per inflorescence were obtained from each study plot in 2006, 2007 (*S. pulchella* only) and 2008. For each study plot, we used the number of individuals blooming in the year when all individuals in the plot were counted (*see* above) to calculate the proportion of flowering individuals in the plot for that year.

At the end of flowering each year, we assessed the fruit set to determine the female reproductive success in each plot. Based on these counts, Lorenz curves (Weiner & Solbrig 1984, Calvo 1990) were constructed for each population sample to visualize the relative annual contributions of flowering individuals to the capsule pool. Individuals were sorted in ascending order by the number of capsules they produced, and the cumulative percent of capsules was plotted

against that of individuals. A diagonal line from the lower left to the upper right corner of the diagram would indicate equal individual contributions, whereas curves deviating from this diagonal line would indicate inequality.

Using the program SigmaStat network version 1.01, we performed one-way ANOVA on ranks (as the data set failed the normality test) in order to test for differences in relative fruit set (pooled over the entire study period) between the three species. Subsequently, we used Dunn's test to reveal which species were mutually different in this respect.

Seeds from dehisced capsules of *S. mirabilis*, *S. monophylla* and *S. pulchella* (30 capsules each) were collected and dried in silica gel. We assessed the number of seeds per capsule by counting them under a low-power binocular microscope. For each species and study year, we calculated the mean number of seeds per inflorescence as the product of (1) the mean number of seeds per capsule, and (2) the mean number of capsules per inflorescence. Furthermore, we estimated the number of seeds produced per individual (flowering or vegetative) in the population sample of each species (for the year with known proportion of flowering individuals) as the product of (1) the mean number of seeds per inflorescence, and (2) the proportion of flowering individuals. Provided that this rate (as well as the population size) is sufficiently stable over several years, it can be used to measure the efficiency of recruitment: the fewer seeds produced per individual (i.e. the fewer seeds required for recruitment of one new individual), the higher efficiency.

To determine the male reproductive success in the population samples of *S. mirabilis* and *S. monophylla*, respectively, we checked 20 and 13 inflorescences for pollinarium removal in 2006. Thus, we recorded the total number of flowers on each inflorescence, together with the number of flowers from which the pollinarium was removed (no flowers were observed in which only one hemipollinarium was removed). Based on these counts, we constructed a Lorenz curve for each population sample to visualize the relative annual contributions of flowering individuals to the pool of pollinaria removed.

In most genera under subtribe Orchidinae, pollinia just extracted from the flower are positioned on the insect so as to strike the anther rather than the stigma of the same or another flower. However, in 30–80 seconds (depending on the species), differential drying of the caudicles will result in bending or twisting that changes the orientation of the pollinia so that they will strike the stigma when the pollinator later visits another flower — an adaptation that increases the rate of allogamy relative to auto- or geitonogamy (Darwin 1862). To test for this adaptation in *Sirindhornia*, we experimentally extracted three pollinaria from each species and kept them under observation for subsequent movements during 10 minutes.

Table 1. Definitions of species-specific size classes for *Sirindhornia mirabilis*, *S. monophylla* and *S. pulchella*, using length of the longest leaf (cm) as general indicator of plant size.

Size class	*S. mirabilis*	*S. monophylla*	*S. pulchella*
1	0.1–5.0	0.1–2.0	0.1–3.0
2	5.1–10.0	2.1–4.0	3.1–6.0
3	10.1–15.0	4.1–6.0	6.1–9.0
4	15.1–20.0	6.1–8.0	9.1–12.0
5	20.1–25.0	8.1–10.0	12.1–15.0
6	25.1–30.0	10.1–12.0	15.1–18.0
7	30.1–35.0	12.1–14.0	18.1–21.0
8	35.1–40.0	14.1–16.0	21.1–24.0

Results

Morphological size correlations and population structure

Our counts of all individuals visible above ground in the study plots revealed 105 individuals of *S. mirabilis*, 120 of *S. monophylla* (both counted in 2006) and 274 of *S. pulchella* (counted in 2007). Inflorescence length was positively correlated with leaf length in both *S. mirabilis* ($r = 0.62$, $p < 0.01$), *S. monophylla* ($r = 0.75$, $p < 0.01$), and *S. pulchella* ($r = 0.67$, $p < 0.01$). The number of flowers per inflorescence was positively correlated with leaf length in *S. mirabilis* ($r = 0.49$, $p < 0.01$) and *S. monophylla* ($r = 0.59$, $p < 0.01$), but not in *S. pulchella*.

Distribution among size classes (*see* Table 1) was rather uniform for all three species. In *S. mirabilis* (Fig. 1A), distribution of plants among size classes resembled a normal distribution, whereas the distribution was skewed to the left in *S. monophylla* (Fig. 1B) and particularly in *S. pulchella* (Fig. 1C). Especially *S. monophylla* had very low numbers in size class 1 (Fig. 1B).

The smallest flowering plants of *S. mirabilis* had a leaf length of 8.5 cm, whereas *S. monophylla* and *S. pulchella* could start to flower when the leaf length exceeded 3.5 cm and 5.0 cm, respectively. The proportion of flowering plants generally increased with plant size in each species, although this trend was not completely consistent (Fig. 1).

Flowering, reproductive success and pollinarium movements

All flowering *Sirindhornia* individuals consistently produced one inflorescence only. Overall relative fruit set (Table 2) depended on the species ($p < 0.001$) and was significantly different ($p < 0.05$) between *S. monophylla* on the one hand and *S. mirabilis* on the other, but not between *S. mirabilis* and *S. pulchella*.

Thirty-six individuals of *S. mirabilis* in the study plot bloomed in 2006 (corresponding to 34.3% flowering). For relative contributions of flowering individuals to the capsule pool in 2006 and 2008, *see* the Lorenz curves (Fig. 2A). In 2006, the overall pollinarium removal rate was 39.9% ± 23.1% (mean ± SD). For relative contributions of individuals to the pool of pollinaria removed, *see* the Lorenz curve (Fig. 3).

Twenty-five individuals of *S. monophylla* in the study plot bloomed in 2006 (corresponding to 20.8% flowering). For relative contributions of individuals to the capsule pool in 2006 and 2008, *see* the Lorenz curves (Fig. 2B). In 2006, the overall pollinarium removal rate was 91.2% ± 10.4% (mean ± SD). For relative contributions of individuals to the pool of pollinaria removed, *see* the Lorenz curve (Fig. 3).

Twenty-three individuals of *S. pulchella* in the study plot bloomed in 2007 (corresponding to 8.4% flowering). For relative contributions of individuals to the capsule pool in 2006, 2007 and 2008, *see* the Lorenz curves (Fig. 2C).

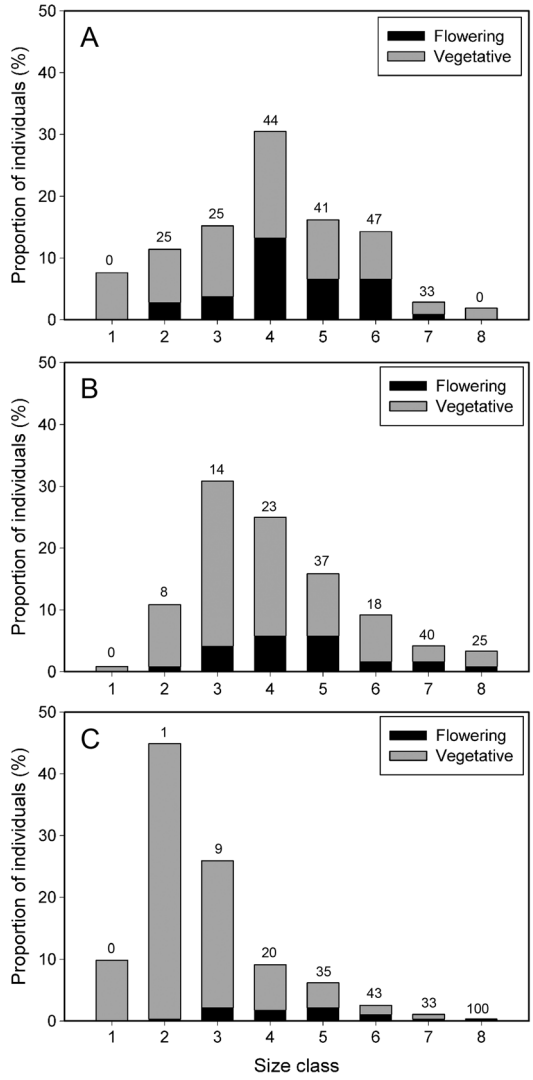

Fig. 1. Distribution of flowering and vegetative individuals among size classes in the study plots. — **A**: *Sirindhornia mirabilis* (2006). — **B**: *S. monophylla* (2006). — **C**: *S. pulchella* (2007). Numbers on top of columns indicate the proportion of flowering individuals within each size class (%). For definitions of size classes, *see* Table 1.

The number of seeds produced per capsule was 5911 ± 1613 in *S. mirabilis*, 1974 ± 902 in *S. monophylla*, and 3075 ± 1134 in *S. pulchella* (both mean ± SD) (*see* Table 2).

No pollinarium movements could be observed.

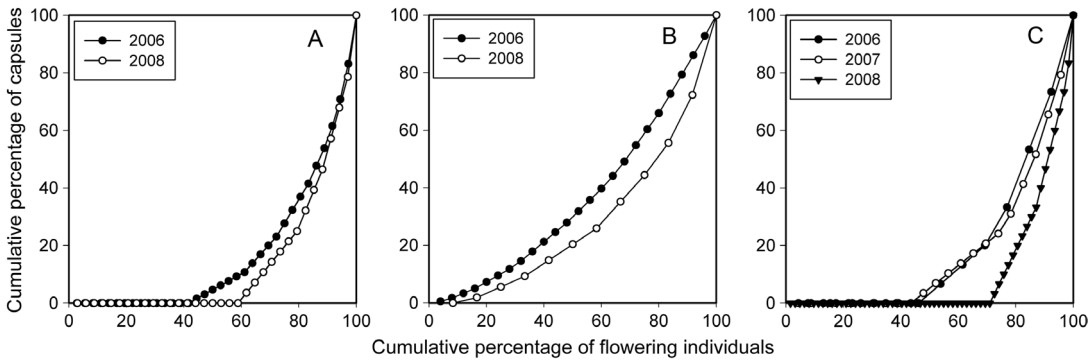

Fig. 2. Lorenz curves illustrating the relative contributions of individuals to the capsule pool in 2006, 2007 (*S. pulchella* only) and 2008. — **A**: *Sirindhornia mirabilis*. — **B**: *S. monophylla*. — **C**: *S. pulchella*.

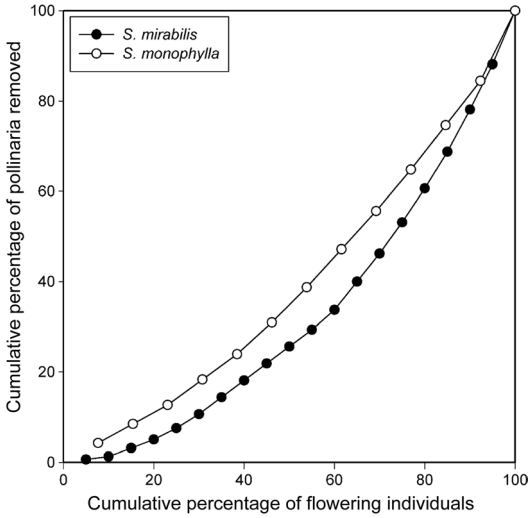

Fig. 3. Lorenz curves for *Sirindhornia mirabilis* and *S. monophylla*; for both species illustrating the relative contributions of individuals to the pool of pollinaria removed in 2006.

Discussion

Demography

The relative distribution of individuals among size classes was rather similar in the populations of *S. mirabilis*, *S. monophylla* and *S. pulchella* (Fig. 1), all being characterized by their low numbers of small and large individuals. Likewise, it was characteristic of all three species (irrespective of the species-specific arbitrary size class definitions) that only size class 1 did not contain any flowering plants, and that the proportion of flowering plants in size class 2 was low. Thus, it can be assumed that size class 1 in each species consists of juvenile plants only, and that size class 2 probably comprises a mixture of juvenile and adult (i.e. potentially flowering) plants, whereas the higher size classes consist entirely of adult plants (partly flowering, partly vegetative).

Table 2. Survey of the number of *Sirindhornia* inflorescences in each study plot, together with the overall relative fruit set (mean ± SD), the mean number of capsules per inflorescence and the mean number of seeds per inflorescence for each study year, and the approximate number of seeds produced per individual (flowering or vegetative) in the population for the study year with known proportion of flowering individuals. *n* = number of inflorescences.

Species	Year	*n*	Relative fruit set (%)	Capsules per inflorescence	Seeds per inflorescence	Proportion of flowering plants	Seeds per individual
S. mirabilis	2006	36	9.6 ± 12.3	1.806	10675	0.343	3662
	2008	34	4.5 ± 7.2	0.824	4871	–	–
S. monophylla	2006	25	51.6 ± 31.2	7.160	14134	0.208	2940
	2008	12	38.0 ± 20.0	4.500	8883	–	–
S. pulchella	2006	13	17.3 ± 20.8	1.154	2278	–	–
	2007	23	25.9 ± 31.0	1.261	3878	0.084	326
	2008	62	11.4 ± 19.7	0.484	1488	–	–

Against this background, the age structure of all three populations seems heavily dominated by adult plants. This can be due to recently decreased levels of reproduction by seed, or it can be due to the adult stage of the plant lasting much longer than the juvenile stage. Judging from the strong variation in age spectra found in populations of numerous terrestrial orchid species (Vakhrameeva & Tatarenko 1998), all studied in undisturbed habitats, and noting the similar spectra that we found on Doi Hua Mot and Doi Chiang Dao ca. 360 km apart, we tend to think that the latter explanation is the more likely, and that a long-lasting adult stage is characteristic of *Sirindhornia*. Vakhrameeva and Tatarenko (1998) studied nine temperate to subtropical orchid species representing the same life form as *Sirindhornia*. Among these, the study populations of *Anacamptis pyramidalis*, *Neottianthe cucullata*, *Orchis mascula* and *Traunsteinera globosa* were likewise dominated by adult plants.

Observing the distribution of individuals among size classes 3–8 (i.e. the classes presumed to consist of adult plants only), a consistent decline according to size class is evident in *S. monophylla* and *S. pulchella* (Fig. 1B–C), probably reflecting an age-related curve of accumulated mortality that is already well known from a range of other orchid species (e.g. Zotz 1998, Winkler & Hietz 2001, Watthana 2005, Watthana *et al*. 2006, Watthana & Pedersen 2008). In comparison, it is puzzling that size class 3 in *S. mirabilis* contains fewer individuals than size class 4 (Fig. 2A). However, such a relatively minor deviation from a consistent decline might well be explained by the circumstance that cohorts of juvenile individuals vary in size between years due to natural variation in growth and reproductive conditions.

Orchids are known to vary widely in flowering frequency, both between species, between populations and between years in one and the same population. Thoroughly studied examples of the latter phenomenon in species with root/stem tuberoids and annual renewal of all organs (as in *Sirindhornia*) include populations of *Anacamptis morio* (Wells *et al*. 1998, Jersáková *et al*. 2002), *Coeloglossum viride* (Willems & Melser 1998), *Dactylorhiza incarnata* and *D. sambucina* (Tamm 1972), *D. majalis* subsp. *lapponica* (Øien & Moen 2002), *Gymnadenia conopsea* (Øien & Moen 2002, Gustafsson 2007), *Herminium monorchis* (Wells 1994, Wells *et al*. 1998), *Neotinea ustulata* (Tali 2002), *Ophrys apifera* (Wells & Cox 1989, 1991), *O. insectifera* (Dorland & Willems 2002), *O. sphegodes* (Hutchings 1987a, 1987b), *Orchis mascula* (Tamm 1972), *O. militaris* (Hutchings *et al*. 1998, Waite & Farrell 1998) and *O. purpurea* (Jacquemyn *et al*. 2002). The above references together propose several factors that might explain the observed flowering dynamics — including resource limitation, temperature, precipitation and light environment. In *Sirindhornia mirabilis*, 36 individuals bloomed in the study plot in 2006 and 34 did so in 2008; in *S. monophylla*, the number of flowering individuals decreased from 25 to 12 between 2006 and 2008; in *S. pulchella*, the corresponding number increased from 13 in 2006 to 23 in 2007 and 62 in 2008. Judging from the population structure as mapped in 2006 (*S. mirabilis*, *S. monophylla*) and 2007 (*S. pulchella*) (*see* Fig. 1), the proportion of flowering plants increased with increasing plant size in all species of *Sirindhornia*. However, this trend was not completely consistent, but due to the low number of individuals in the highest size classes, it is not possible to decide if the divergent patterns in especially size classes 7–8 are characteristic or fortuitous. Perhaps, a senility factor causes a generally decreased probability of flowering among the oldest individuals. Monitoring of individual plants over several years would be needed to decide whether flowering dynamics in the three species of *Sirindhornia* are governed primarily by climate, resources or age.

Individual contributions of progeny

The Lorenz curve based on pollinarium removal in *S. mirabilis* (Fig. 3) is skewed to the right, indicating unequal contribution of individuals to the pool of pollinaria removed. It differs from the corresponding Lorenz curve for *S. monophylla*, which forms a nearly diagonal line from the lower left to the upper right corner, indicating almost equal individual contributions.

The Lorenz curves based on fruit set in *S. mirabilis* and *S. pulchella* (Fig. 2A and C) are

strongly skewed to the right and much more similar to the curves that Calvo (1990), Pedersen *et al*. (2004), Watthana *et al*. (2006) and Watthana and Pedersen (2008) provided for allogamous orchid species than to the curve that Calvo (1990) provided for the autogamous *Oeceoclades maculata*. In contrast, the Lorenz curves based on fruit set in *S. monophylla* (Fig. 2B) are less skewed to the right, so they indicate more equal contributions of individuals to the capsule pool. If compared to the curves provided by Calvo (1990), *S. monophylla* could be assumed to be autogamous. However, recent pollination experiments demonstrated that this is not the case (Srimuang *et al*. 2010); the only slightly skewed condition of the Lorenz curves simply reveals a consistently high pollination success in an insect-pollinated species.

The unequal distribution of capsules (Fig. 2) among individuals, particularly in the populations of *S. mirabilis* and *S. pulchella*, accounts for differences in the female genetic contribution of progeny. If the same individuals continue to be the most important contributors during a number of years, this might influence the genetic composition of the populations. The almost identical curves that we obtained for each species during two or three years (Fig. 2) suggest that the degree of (in)equality is fairly constant and partly species-specific in *Sirindhornia*, but our data do not reveal whether the same individuals have been the most important contributors every year.

A possible high rate of full sibness (resulting from one pollinarium fertilizing all ovules in an ovary) might account for a correspondingly unequal male genetic contribution, especially when taking into account the unequal contributions of pollinaria among individuals of particularly *S. mirabilis* (Fig. 3). However, it should be remembered that the pollinia of *Sirindhornia* are composed of fairly loosely assembled massulae. Each pollinarium can probably pollinate several flowers by leaving minor clumps of massulae rather than entire pollinia on individual stigmas (cf. Neiland & Wilcock 1995, Singer & Cocucci 1997, Singer 2001).

By reducing pollen carryover from one individual to another, geitonogamy can reduce the male fitness of a plant. As we found no bending mechanism in experimentally extracted pollinaria from *Sirindhornia* flowers, the species of this genus must be more prone to geitonogamy (cf. Johnson & Nilsson 1999). Consequently, we expect the populations of all three species to accommodate low levels of heterozygosity and genetic variation.

Relations between fruit set, seed production and recruitment

Low relative fruit set is commonly found in allogamous orchid species (e.g. Calvo 1990, Neiland & Wilcock 1998, Huda & Wilcock 2008). In *Sirindhornia*, we generally found the narrowly endemic *S. mirabilis* and *S. pulchella* to have lower relative fruit set than the more widely distributed *S. monophylla* (Table 2). However, the number of seeds per capsule seems to be negatively correlated with the (species-specific) relative fruit set in *Sirindhornia*. Thus, *S. monophylla* exhibited the highest relative fruit set (38.0%–51.6%), but had the lowest number of seeds per capsule (1972 ± 902), whereas *S. mirabilis* exhibited the lowest fruit set (4.5%–9.6%), but produced the highest number of seeds per capsule (5911 ± 1613). As proposed by Calvo (1990), a high number of seeds per capsule may help to counterbalance low fruit set. This is clearly seen in *Sirindhornia* where the mean number of capsules produced per inflorescence in *S. mirabilis* was 12%–19% of the level in *S. monophylla* in 2006–2008, whereas the corresponding figure for seeds per inflorescence was 55%–76% in the same period (Table 2).

Although one *Sirindhornia* fruit typically contains ca. 2000–6000 seeds, depending on the species, successful germination must rely heavily on environmental factors like in other orchids (cf. Rasmussen 1995). We found the relation between total estimated seed production and population size (above ground) to differ widely between the three *Sirindhornia* species (Table 2); in *S. pulchella* only 326 seeds were produced per individual in the study population (in 2007), whereas the corresponding rates for *S. mirabilis* and *S. monophylla* (in 2006) were 3662 and 2940, respectively. Thus, recruitment appears

to be more efficient in *S. pulchella*. At least four possible explanations exist. First, a considerably higher proportion of the dispersed seeds may be lost without germinating in *S. mirabilis* and *S. monophylla*, either as a result of fundamentally different soil seed-bank dynamics (cf. Batty *et al.* 2000, Whigham *et al.* 2006) or because of lower densities of unsaturated microsites suitable for germination (cf. Eriksson & Ehrlén 1992, Jersáková & Malinová 2007). Second, mortality of the youngest, completely subterranean stages may be much higher in *S. mirabilis* and *S. monophylla*. Third, a much higher proportion of individuals in the two latter species (relative to *S. pulchella*) may be subterranean at any one time (in which case, population sizes are more strongly underestimated for these species than for *S. pulchella*). Fourth, the study populations may not be stable; if the population of *S. pulchella* is declining rapidly, and/or if the populations of *S. mirabilis* and *S. monophylla* are growing rapidly, the calculated figures simply give an erroneous impression of the magnitude of recruitment of adult individuals in relation to seed production (however, we are not aware of such dramatic changes in population size for any of the three species). Long-term monitoring of the populations (Whigham & Willems 2003) combined with *in situ* germination experiments (Rasmussen & Whigham 1993, 1998) are needed to achieve a better understanding of the phenomenon.

Conclusion: reproductive restrictions in relation to geographic range

Whereas all three species exhibited rather similar patterns with regard to demography in the sampled populations, we found the widespread *S. monophylla* to be characterized by more equal individual contributions of progeny (Figs. 2–3), higher relative fruit set and higher seed production per inflorescence (Table 2). Thus, in most respects where the three species differed, the local endemics were more reproductively restricted than their widespread relative. However, this pattern was not universal, as recruitment appeared to be more efficient in *S. pulchella* than in the other two species.

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