



Comparison of population structures and ecology of a congeneric pair of common and rare neotropical tree species

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Abstract

We compared the general ecology and population profiles of *Jatropha standleyi* and *J. chamelensis*, two ecologically similar, dioecious forest trees in order to illuminate why they differ in range size, an important measure of relative commonness and rarity. *Jatropha standleyi* is widespread throughout the tropical deciduous forest in Mexico and the endangered *J. chamelensis* is restricted to a small region on the Pacific coast of Mexico. Using data collected over the same time period from a site central to the distributions of both species, we found significant differences in population size distributions and seedling mortality, but no discernible differences in seedling or adult growth rates, local abundance or local distribution. The observed difference in relative rarity could be explained by a number of hypotheses depending on whether the populations are at a stable equilibrium or not. The high ratio of pre-reproductive individuals may indicate a growing, rather than stable, population for *J. chamelensis*. *Jatropha standleyi* is more widespread and has a significantly lower ratio of pre-reproductive to mature individuals. Alternatively, both populations may be at equilibrium with *J. chamelensis* restricted to its limited range by large-scale environmental constraints or niche differences not elucidated in this study. In either case however, the greater and less variable seed output of the *J. standleyi* population will also mean a greater number of rare long-distance dispersal events and a better chance of establishing a persistent remote population for *J. standleyi* than for *J. chamelensis*. The dioecy to be found in both these species would exacerbate the limiting effects of low seed production on the ability of a species to ‘travel’ successfully. A more extensive field investigation of mortality and factors contributing to mortality in sub-canopy and pre-reproductive individuals would allow more light to be shed on relative population processes in these species.

Introduction

Multi-species analyses have produced several general patterns with regard to commonness and rarity as it relates to range size in plant species. In British plants, animal pollinated species are less widespread than wind pollinated species, tree species are less widespread than shrub species, and clonal species have smaller range sizes than non-clonal species when taxonomic relatedness is taken into account (Kelly 1996; Kelly and Woodward 1996). Approaching the question somewhat differently, cross-species analyses

have found more widely distributed species to be more locally abundant, and explain this result as a function of greater niche breadth in common relative to rarer species (Guo et al. 2000; Hengeveld and Haeck 1981, 1982). Lastly, Rabinowitz (1978) showed prairie grasses of lesser abundance to have more ‘dispersible’ propagules than commoner species giving them the potential to exploit spatially or temporally rare micro-sites. Eriksson and Jakobsson (1998) recently has attempted to translate this observation into explicit expectations of a relationship between regional distribution and seed size. Nonethe-

less, by and large, ecological understanding of the causes and consequences of plant species rarity is in its early stages.

This is especially true for the understanding of rarity in trees, a cause for some concern. In even the most common tree species, the sheer physical size of an individual dictates a relatively small number of reproductive adults in any one population, and a greater risk of extinction just by chance alone (May et al. 1995). Defining traits of trees such as longevity, resource storage and irregular and long-lived reproductive schedules make extrapolation of data from herbs inappropriate and makes tree demographics difficult to study in relation to the duration of normal research projects or grants. Through their large physical size, trees influence the physical environment, and at the level of individuals and populations, play a large role in community function through the support of dependent animals (Kelly and Southwood 1999; Kennedy and Southwood 1984; Southwood 1960, 1961). Thus a greater understanding of rarity in trees would be of value in filling a largely unwritten chapter in basic ecology, and of relevance in the understanding and preservation of communities and biodiversity.

Whilst multi-species analyses are useful in generalising observations and testing hypotheses, such analyses have necessary limits on the depth and type of biological information that can be included. Illumination of the processes that produce or disrupt general patterns may be more effectively reached through the study of a model system. However, rarity is an inherently comparative phenomenon, depending fundamentally on the underlying biology and ecology of an individual taxon – what is numerous or widespread for one taxon may be sparse or restricted for another – and therefore a species is best described as common or rare in comparison to another, otherwise similar species. For this reason, we have chosen for our model system a congeneric pair of ecologically similar, common and rare species as a means of minimising the number of extraneous factors that may cause species to differ (Harvey 1996; Harvey and Pagel 1991). Our study further reduces the number of potentially confounding effects through comparison of the two species at the same site and point in time in order to provide the clearest evidence possible of how observed differences between the two target species may be functionally related to differences in commonness and rarity.

In the study reported here, we have compared the ecology and population structures of *Jatropha stand-*

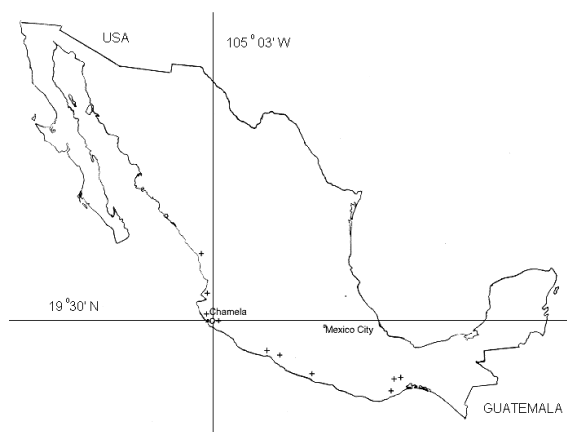


Figure 1. Map of México showing ranges of *J. standleyi* (+) and *J. chamelensis* (o). Points represent sites of collection for taxonomic purposes and should not be taken to signify individual populations. Several collections may have been, and usually were made from the same general site, although not necessarily at the same point in time. Prior to the second half of the 20th century, the tropical deciduous forest of the Pacific coast of México is considered to have been fairly continuous, and even today the middle portions remain relatively uninterrupted. In consequence, and given the distance neotropical insect pollinators are capable of travelling between individual trees (Boshier et al. 1995), the range of *J. standleyi* may represent what has historically been a species gradient rather than a series of independent populations. Points on the map are for visual representation only. Range position was calculated directly from latitudinal data.

leyi Steyererm. and *J. chamelensis* Pérez Jiménez (Euphorbiaceae), native species occurring naturally at the centre of their distributions at the Estación de Biología Chamela on the Pacific coast of Mexico. Endemic to the Chamela region, *J. chamelensis* is endangered at a global level (Walter and Gillett 1998); *J. standleyi* is distributed throughout the tropical deciduous forests of the Pacific coast of México (Figure 1). One previously reported difference between these two species is in the size of their seed crop (Pirie et al. 2000), with the restricted species producing a smaller seed crop than the widespread species. We expanded on this comparison by looking for differences in seedling and adult growth rates, seedling mortality and population size distributions which may explain why one species is widespread (common) and another is restricted (rare).

Methods

The study species

Both *Jatropha chamelensis* and *J. standleyi* are deciduous forest canopy emergents restricted to tropical deciduous forest (typology of (Rzedowski 1978)). A distinctive tree up to 10 m in height, *J. chamelensis* has golden yellow exfoliating bark and large cordate or circular leaves up to 30 cm in length. *Jatropha chamelensis* is classed as endangered at the global level (Walter and Gillett 1998) and is endemic to Chamela, the only known specimens being from the Estación de Biología Chamela and immediate surrounding area (Figure 1). The more widespread *J. standleyi* may reach 8 m in height, and it has bark that is indistinguishable in colour and texture from the bark of *J. chamelensis*. The leaves of the two species are distinct, however; the oblanceolate leaves of *J. standleyi* are at most 2/3 the length and approximately 1/3 the area of *J. chamelensis* leaves. The clear yellow sap of *J. standleyi* further distinguishes its seedlings and saplings from those of *J. chamelensis* and other superficially similar species. Thus, even the smallest seedlings are easily identified to species. Both species are dioecious (Bullock 1985) and ripe fruits are green. The fruit has either two or three lobes 3–5 cm in diameter although three-lobed fruit are more common for *J. chamelensis* whilst two-lobed fruit are more common on *J. standleyi*; no fruit have been observed to contain more than one seed in a lobe. The seeds of both species are visually indistinguishable from each other and are approx. 1–1.5 cm in diameter (Pirie et al. 2000). The two species may hybridise to produce a shrub or tree with three-lobed leaves and two- or three-lobed fruit (Lott 1993); such hybrids have been observed only rarely at Chamela (YMB, pers. obs.). Neither species is known to exhibit clonal growth or produce vegetative propagules.

The Estación de Biología Chamela (a facility of the Instituto de Biología, Universidad Nacional Autónoma de México) is located in the state of Jalisco on the Pacific slope of the Sierra Madre del Sur at approximately 19°30' N, 105°03' W. The reserve covers 1600 hectares and the portion of the reserve used in this study incorporates an elevational range of 30–200 m above sea level. The average annual precipitation of 748 mm falls over a 5 month rainy season (mid-June to mid-November (Bullock 1986)). The field season in 1998 followed a severe El Niño event, with the preceding dry season beginning a

month and a half earlier than usual, in early October. The predominant vegetation is tropical deciduous forest, with some bands of tropical semi-deciduous forest along river beds.

Geographic distributions

Chamela is central in the geographical ranges of both species. Natural occurrences of both species have been reported only from tropical deciduous forest. Geographic and habitat distributions were determined from a total of 61 specimens in the collections of the Estación de Biología Chamela and the Herbario Nacional MEXU and the herbaria of the University of Michigan (R. Rabeler, pers. comm.), the Royal Botanic Gardens, Kew (P. Hoffmann, pers. comm.), the Missouri Botanical Gardens W³ specimen database (2000) and the United States National Herbarium (R. Russell pers. comm.). As *J. standleyi* may be synonymous with *J. sympetala* S.F. Blake and Standl. (S. Bullock, pers. comm.), specimens with this name were also included. No other specimens were located for these two species. The relative range positions of the Chamela populations were determined by dividing the latitude range for each species into quarters and determining the quarter containing the Chamela reserve. Longitude was not figured into the estimate of range size: east-west distributions of *J. standleyi* follow the occurrence of tropical deciduous forest, which is dictated by the shape of the Pacific coastline rather than by any independent effect of longitude.

Local distributions and abundances

Local distributions and abundances for canopy emergent individuals (those > 3 cm diameter at breast height; close to or in the canopy of this low forest) of each species were calculated from mean occurrence in 14 permanent plots (30 m × 80 m). The 14 plots were established to characterise vegetation in relation to elevation in the study area between 1985 and 1999 and are distributed along five small canyons. In four out of five of the canyons, plots were located at three elevations, the higher overall elevation of the fifth canyon allowed plots only at intermediate and high elevations, a sampling regime intentionally designed to span and replicate the range of conditions present at Chamela. All trees within the plots greater than 3 cm dbh (diameter at breast height) were tagged, mapped and identified. Plots contained between 630

and 1,050 individuals each, for a total of approximately 11,500 identified trees in 190+ species.

Differences in 'habitat preferences' were investigated in two ways. First a contingency table was drawn up and Fisher's exact test (Crawley 1993) was used to determine whether the two species co-occurred more or less than you would expect by chance, i.e. a significant interaction between the presence or absence of *J. standleyi* and the presence or absence of *J. chamelensis* in a plot. Secondly a generalised linear model (GLM; S-Plus 4.5 Mathsoft 97) was used to determine whether the two species differed in their distribution between elevations (high, medium and low) within the canyons, i.e. whether the interaction between species and elevation was significantly different from random. As we were dealing with count data Poisson errors were used and as the data were over-dispersed an F-test was used when comparing models for significance (Crawley (1993), S-Plus 4.5 Mathsoft 97).

Seedling growth and mortality

Seedling mortality rate was examined using an independent data-set comprising seedlings gathered from areas outside the permanent plots and in the general vicinity of but outside those areas used for profiling the populations. Site choice thus minimised potential trampling effects. Data concerning growth and mortality of 233 seedlings (117 *J. standleyi* and 116 *J. chamelensis*) were collected in July 1996 and July 1997. Seedlings were located predominantly near paths used only for research purposes within the Station boundaries. Seedling height was measured to an accuracy of 5 mm; seedling diameter was measured with a Mitutoyo digital caliper to an accuracy of 1 mm. Seedling death was confirmed by location and recovery of tags in the second season of observation.

Correlates of seedling survival from 1996 to 1997 were identified using a generalised linear model (GLM; SPLUS 4.5, Mathsoft 1997). Seedling survival was designated as the binary response variable; initial size and species identity were entered into the model as possible explanatory variables. Any error in the model was assumed to have a binomial distribution. The analysis was performed using the logit link function with a binomial denominator of 1.

A GLM was also used to ascertain the determinants of seedling growth. For this analysis, seedling size in 1997 was designated as the response variable and initial size and species identity as the explanatory

variables. Dead seedlings were excluded from this analysis. In order to normalise the residuals, the variance term was set to increase with the mean. Interaction terms were fitted and tested for both the growth and survival models. The relative importance of the explanatory variables was determined by deleting each variable from the full model and obtaining an estimate of the significance level of the variable from the resulting change in deviance (Crawley 1985). An F-test was used for the growth model and a χ^2 test for the survival model.

Adult growth and mortality

For many tree species, different patterns of growth develop once an individual emerges from beneath the canopy. Adult growth rates were calculated for 17 *Jatropha* individuals (8 *J. chamelensis*, 9 *J. standleyi*) ≥ 3 cm dbh found on the permanent plots. Of the seven plots established in 1987 and re-censused in 1998–1999, four contained individuals of the target species, all four plots were at intermediate elevations. Initial measurements were collected in 1987; using maps accurate to 0.5 m, individuals were relocated and remeasured in 1998 or 1999. Size data from these individuals were used to estimate growth rates. Correlates of and differences between the two species in growth rates were determined using a GLM. The model was constructed assuming error to be normally distributed and with quadrat membership (site), initial tree size (log transformed) and species identity as potential explanatory variables for average annual growth in diameter (log transformed; SPLUS 4.0, Mathsoft 1997). Over the course of the 11–12 yr interval separating the two measurements, three *J. standleyi* and no *J. chamelensis* died. Adult mortality was considered to be too low for statistical analysis.

Population size distributions

Data concerning population structure of individuals within the reserve boundaries were collected from early August to mid-September 1998 for both *J. standleyi* and *J. chamelensis*. As individuals were widely dispersed in the forest, seedlings and adults of both species were sought initially from paths and stream-beds, with forays further into the vegetation in order to more completely assay populations observed from the trails. In total, 348 individuals of *J. standleyi* and 358 individuals of *J. chamelensis* were included in the demographic study. Approximately

equal numbers of individuals were located to construct population profiles; these numbers were not intended to reflect the relative abundances of the species at the site.

To ensure that individuals were counted only once and relocated in future seasons each individual was tagged with an identifying code. The height of individuals less than 2.5 metres tall was recorded, and girth at breast height (133 cm from the ground) of all taller individuals was measured and noted. If individuals had more than one trunk at breast height, girths of all trunks were measured, converted to basal areas, summed and then converted back to a single diameter measure. Some of the smallest seedlings located still possessed cotyledons, indicating that the data set encompassed the full complement of seedling sizes.

We investigated differences in size distribution patterns, which could shed light on life-history differences, by sorting the two species into size categories using the same criteria for each, with individual size as the axis along which categories were arranged. For the purpose of constructing the size profiles, girth measurements were converted into diameter values for all individuals greater than 2.5 m in height. Girth differences between plants < 2.5 m tall were small and all individuals in this class had a dbh much less than 3 cm. A diameter of 3 cm or greater indicated an individual that may have attained canopy height and therefore 3 cm defined the upper limit of the smallest size category. All other size categories comprised equal, 2 cm increments. The non-parametric Kolmogorov-Smirnov test was used to test for gross differences between the population size distributions. The Kolmogorov-Smirnov test is sensitive to differences in location, dispersion and skewness of the two distributions (Sokal and Rohlf 1995).

We also examined population size distributions more closely by asking two questions aimed at illuminating potential population processes without violating the strictures imposed by static data (Condit et al. 1998; Fox and Gurevitch 2000). We used proportion tests to test whether the two populations differed in the relative proportions of sub-canopy versus canopy emergent individuals and keeping in mind the result that the two populations did not differ in local abundance, we tested whether the two species differed in the ratio of pre- versus potentially reproductive canopy emergent individuals. Pre-reproductive individuals were classed as all those smaller than the smallest individual observed fruiting, potentially reproductive individuals were not observed fruiting but

were as large as or larger than the smallest individual observed fruiting. The proportion test assumes a binomial model for each group, with the null hypothesis being that both proportions are equal, p-values based on the χ^2 test statistic are two-sided (S-Plus 4.5 Mathssoft 97).

Sex ratio

All individuals marked in the population size distribution study were also examined for presence of fruit, confirming the sex as female. Because flowering had for the most part finished by the time the study was initiated, males could not be distinguished from non-fruiting females. The number of individuals observed fruiting was converted to a proportion of the total number of potential reproductives in each population and compared using a proportion test in order to see if this measure of sex ratio differed between the species.

Results

Commonness and rarity in the study species

Twenty one individuals of *J. chamelensis* were distributed among the 14 permanent plots in 1999, and twenty individuals of *J. standleyi*, this difference was not significant ($F_{1,27} = 0.116$; $P = 0.74$). The number and distribution of individuals between plots is given in Table 1. Although these might be a relatively small numbers of individuals from which to calculate density in less diverse temperature zone forests, it is not an atypical sample size for tropical systems (cf. Condit et al. (1998)) and we have confidence in our result for several reasons. First, we have assessed density from a sampling regime intentionally designed to span and replicate the range of conditions present at Chamela. Second, the values are based on a census of every stem present in a substantial area (2400 m² per plot) rather than the point or transect estimates that may function in less diverse forests. Lastly, there is no evidence for either species of the sort of dispersed 'clumps' of individuals that could lead to a bias from our sampling method; both species are widely distributed among the plots (Table 1) which agrees with our observation of these species in the forest at large. Indeed, the two species cannot be inferred to differ in their distributions within the reserve, the two species occur apart from each other

Table 1. Distribution of individuals among plots. a. Number of plots in which one or more individuals occur at each elevation, also given are the number of plots where both species co-occur. b. Total number of individuals at each elevation.

a.				
Elevation	Total	<i>J. standleyi</i>	<i>J. chamelensis</i>	Co-occurrence
Low	4	2	2	2
Intermediate	5	2	3	2
High	5	0	1	0
b.				
Elevation	<i>J. standleyi</i>	<i>J. chamelensis</i>		
Low	8	8		
Intermediate	12	8		
High	0	5		

Table 2. Results of a generalised linear model determining habitat preference of both species with number of individuals as the response variable.

Parameter	<i>F</i>	<i>P</i>
Species *elevation	3.33	0.059
Elevation	2.85	0.08
Species	0.017	0.897
Canyon	10.25	0.0001

less frequently than that expected by chance alone (2 plots out of 14, in a two-tailed Fisher's exact test $P = 0.015$). Neither species appeared to show any evidence of habitat 'preference' in terms of elevation, however the species *elevation interaction term was only marginally insignificant ($P = 0.059$, see Table 2) and as it is based on such a small sample size this result is inconclusive.

Seedling growth and mortality and adult growth rates

The GLM used in this analysis revealed that seedling mortality within this sample differed significantly between the two species. Both species identity ($\chi^2 = 19.8$, 1 d.f., $P < 0.001$) and initial seedling size ($\chi^2 = 4.0$, 1 d.f., $P < 0.05$) had a significant effect on seedling survival. Mortality in *J. standleyi* seedlings was more than five times that of *J. chamelensis* (27% (31/117) vs 5% (6/116)). *Jatropha chamelensis* seedlings, and larger seedlings of either species, were more likely to survive to the next year, see Figure 2. The interaction between species and size was not significant.

Seedling size in 1997 did not differ between the two species ($F_{1,193} = 3.1$, $P = 0.08$; Figure 2). Only initial seedling size showed a significant positive effect on size the following year ($F_{1,193} = 4055.79$, $P < 0.00005$); this effect did not differ between species (i.e., there was no significant interaction between initial seedling size and seedling identity; $F_{1,193} = 1.49$, $P = 0.2$, see Figure 3). Seedlings used for both growth and mortality analyses ranged in height from 19 cm to 2.5 m and were therefore representative of the smallest class of the population level size distributions. This was a size, not an age, class and therefore could not be assumed to be limited to first year seedlings.

Adult growth rates did not differ significantly between the species ($F_{1,14} = 0.86$, $P = 0.37$) or with initial size ($F_{1,14} = 1.09$, $P = 0.3$). However growth rates varied significantly among plots ($F_{3,14} = 4.64$, $P = 0.019$). Because the two species did not co-occur in all plots used in this analysis, interaction terms were not fitted, all of the plots for which growth data were available were at the same elevation therefore the effect of elevation on growth could not be tested.

Population size distributions

The two species differed significantly in the distribution of individuals among the 14 size classes produced by the sorting algorithm (Kolmogorov-Smirnov $D_{\max} = 0.233$, $p < 0.01$, $n_1 = 348$, $n_2 = 358$; Figure 4). The Kolmogorov-Smirnov test is sensitive to differences in location, dispersion and skewness of the two distributions (Sokal and Rohlf 1995), but our additional tests narrow in on potential bases for this result. Looking more closely at patterns of difference

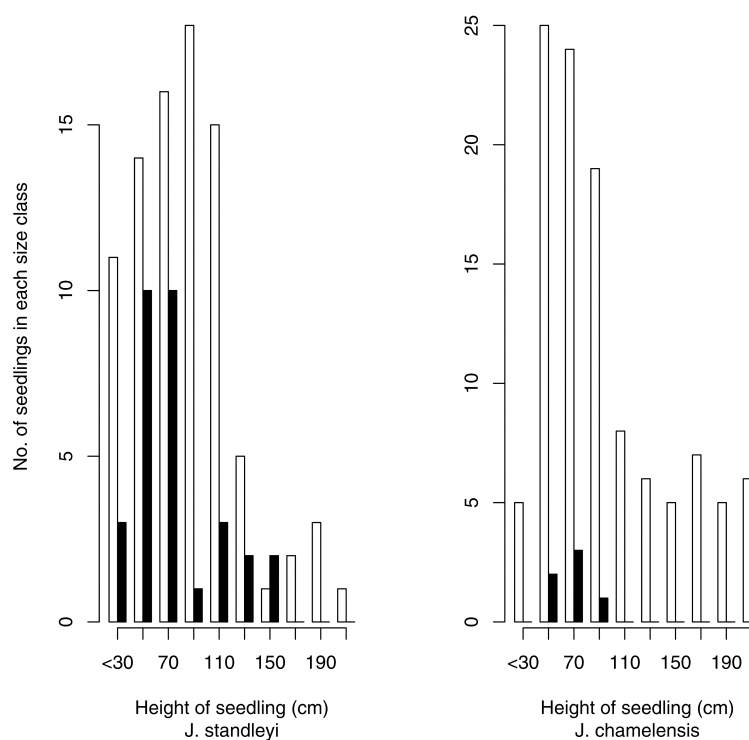


Figure 2. Seedling mortality in relation to species and size. *Jatropha standleyi* is shown on the left and *J. chamelensis* on the right, seedlings alive after one year are represented by the white bars and dead seedlings by the black bars, *J. chamelensis* seedlings ($P < 0.001$, $n = 116$) and larger seedlings ($P < 0.05$) are more likely to survive than *J. standleyi* ($n = 117$) seedlings and smaller seedlings.

between size profiles, we found no significant difference between the species in the proportion of seedlings/saplings in each population. However, *J. chamelensis* had a greater proportion of its canopy emergents in the pre-reproductive size classes than did *J. standleyi* (see Table 3).

Sex ratio

Using the 1997 population distribution data, the minimum size at which individuals were observed fruiting was 8 cm dbh for *J. chamelensis* and 8.1 cm dbh for *J. standleyi*. The proportion of potentially reproductive individuals (i.e. all those trees ≥ 8 cm dbh) observed fruiting in 1998, cannot be inferred to differ between the two species (Table 3). Therefore the two species do not differ in their sex ratios.

Discussion

It has been argued that a species' distribution is the ultimate measure of its 'niche,' in that distribution synthesises the myriad responses that make up a spe-

cies' capacity to survive and reproduce under a particular set of conditions (MacArthur 1972). In this manner, distribution reflects the relative importance in nature of those responses that may (or may not) vary under controlled conditions, and of those complex interactions not amenable to experimental quantification. Indeed, although the absence of a species from a site or habitat may not indicate that the species cannot tolerate those conditions, the presence of a species signifies that it can. If the species can further reproduce and persist over generational time at that site, it may be inferred that local conditions fall within the limits of the niche of the species. The assumption that distribution reflects niche requirements lies behind the proposal that niche breadth determines the observed cross-species correlation between range size and abundance (Brown 1984; Gaston et al. 1997; Hengeveld and Haack 1981, 1982).

Cross-species correlations notwithstanding, we found no evidence that the observed difference in range size between *J. standleyi* and *J. chamelensis* derives from any inherent difference in niche breadth. Although both species may be judged central in their respective ranges and thus under conditions likely to

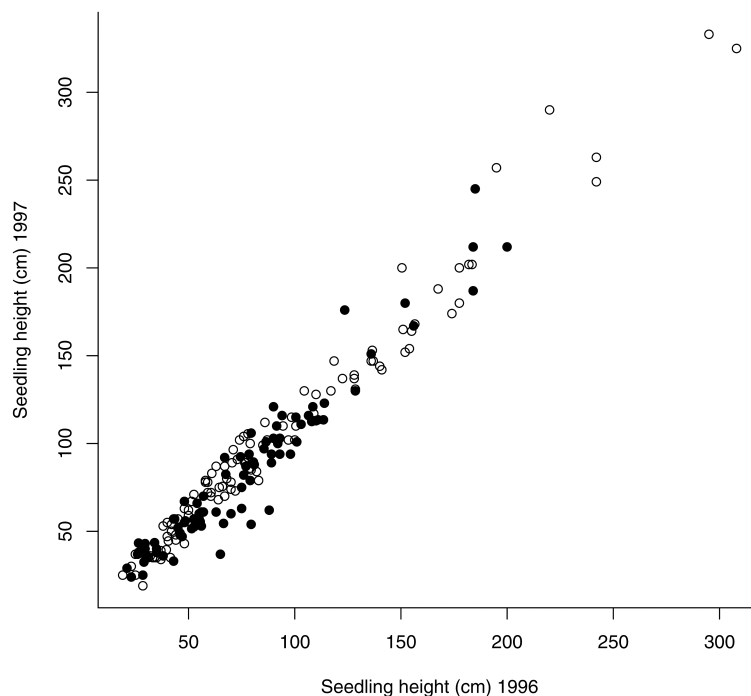


Figure 3. Seedling growth of *J. standleyi* and *J. chamelensis*. No significant difference between the species was found.

be maximally favourable to them, the more widely dispersed *J. standleyi* did not show greater abundance at Chamela than the endemic *J. chamelensis* or a significantly higher individual growth rate at either the seedling or adult stage. Further, the two species co-occurred significantly more frequently than expected by chance, another indicator of underlying similarity in their niches. The finding of co-occurrence is especially notable given the relatively small sample size available for this analysis (14 sites) and the consequent likelihood of obtaining an inconclusive rather than a significant result. Lastly, neither species showed any evidence of habitat 'preference' within the reserve, nor was there any appearance of differences between the two species in distributions of individuals among plots that might not be revealed by statistical analyses (Table 1).

The above results also indicate that the two species are not readily differentiable in terms of life-history 'strategies,' nor is there any evidence of the relationship between propagule morphology and range size that has been suggested as a functional attribute behind commonness and rarity in plants. Originally, Rabinowitz (1978) proposed that differences in commonness and rarity are fostered by smaller propagules of rarer species more readily dispersing to ephemeral patches. That is, rare species are 'colonizing' species

at a temporal or spatial level. Eriksson and Jakobsson (1998) extended Rabinowitz's idea that smaller, more 'dispersible' propagules indicate a colonizing 'strategy,' to propose that the two traits underlie plant commonness and rarity at the regional level (i.e., range size). At Chamela, not only are there no notable differences between the two congeners in propagule morphology, but a previously reported investigation explicitly comparing dispersal modes in *J. standleyi* and *J. chamelensis* found no discernible differences between the two species in this process (Pirie et al. 2000). For both species, a ripe fruit drops to the ground immediately beneath the parent tree; the fruit then rots or is torn apart and dispersal is through removal of individual seeds from the vicinity of the parent. Tooth and claw marks on the seeds that remain, together with the general pattern of removal, indicate that removal is principally by small mammals. Statistical analyses established that *J. standleyi* and *J. chamelensis* seeds possess the same temporal pattern and probability of removal from beneath the parental canopy. Additionally, the presence of a fruit-bearing neighbour had the same significant positive effect on probability of seed removal regardless of whether that neighbour, or the focal individual, is *J. standleyi* or *J. chamelensis* (Pirie et al. 2000).

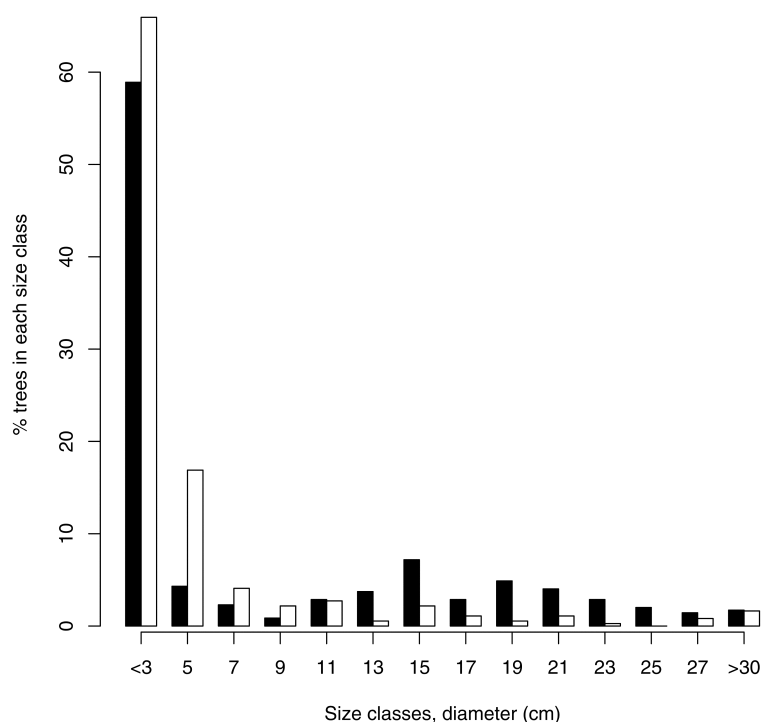


Figure 4. Population structure of *J. standleyi* (common), $n = 348$, shown in black and *J. chameleensis* (rare), $n = 358$, shown in white. The bar plot shows size classes (diameter in cm). The distributions are significantly different according to a Kolmogorov-Smirnov test ($p < 0.01$), with a greater proportion of *J. chameleensis* in the pre-reproductive size classes and with *J. standleyi* predominating in the reproductive size classes. Minimum size of reproduction is within the 9 cm diam. class.

Table 3. Proportion tests of each species' population in three categories; 1. seedlings/saplings (proportion of sub-canopy individuals (< 3 cm dbh) out of total population), 2. pre-reproductive canopy trees (proportion of pre-reproductive trees (> 3 cm & < 8 cm dbh) out of canopy population (> 3 cm dbh)) and 3. reproductive canopy trees (proportion of observed fruiting trees out of potentially reproductive population (> 8 cm dbh)).

	Seedlings/saplings	Pre-reproductive canopy trees	Reproductive canopy trees
<i>J. standleyi</i>	58.9%	16.1%	35%
<i>J. chameleensis</i>	66.2%	68.6%	29%
Proportion test	$\chi^2 = 3.7$, 1 d.f., $p = 0.054$	$\chi^2 = 36.7$, 1 d.f., $p < 0.0005$	$\chi^2 = 0.2416$, 1 d.f., $p < 0.62$

What, then, might be determining the observed differences in range size between *J. standleyi* and *J. chameleensis*, and what support or insight might be derived from the ecology of these two species at Chamela? Possible answers depend on the central issue of whether the two populations are at equilibrium or if one or both populations are expanding at the present time. One possible explanation of the observed difference in range size is that *J. chameleensis* may be expanding from a small population size and restricted range. Potential support for this expansion theory lies in the larger proportion of *J. chameleensis* individuals in pre-reproductive than in potentially reproductive size classes than is the case for *J. stand-*

leyi. Condit et al.'s (1998) test of how size distributions correlate with population growth suggested that static information alone is not a good predictor of future trends and therefore we cannot attach any real weight to this theory. The application of coalescent techniques to genetic data on these two species may enable the construction of a history and better estimate of generational time for *J. standleyi* and *J. chameleensis* at Chamela (Nee et al. 1995; Pybus et al. 1999).

Inspection of the population profiles would also deem it possible that the Chamela populations of both species are stable at or near the densities that we have documented in our study, albeit operating under

somewhat different dynamics to one another, as follows. Although *J. chamelensis* has a lower seedling mortality rate than *J. standleyi*, *J. chamelensis* also has disproportionately fewer reproductive individuals (individuals >8 cm dbh) in an adult population of the same density as *J. standleyi*. Additionally, those adults of *J. chamelensis* that are capable of seeding set significantly fewer seed per individual (mean = 40 seeds versus 23 seeds, $p = 0.026$; Pirie et al. (2000)). With no seed bank at Chamela for either species (J. MacPherson *et al.*, unpub. data) and highly irregular year-to-year fruit set (Bullock and Solis-Magallanes 1990), even in the face of its low population level seed production, *J. chamelensis* may reliably persist at Chamela through its substantial seedling and sapling bank. In contrast, with a greater individual and population seed crop (as above) and less severe year-to-year variation in fruiting patterns (Bullock and Solis-Magallanes (1990); S. Bullock, pers. comm.), *J. standleyi* would be better able than *J. chamelensis* to replace itself through on-going seed production.

This latter point of difference in population seed crop size may also speak to the original purpose of our study, that of identifying potential causes of the observed difference in range size between these two species. For either of the two proposed population dynamic models, the greater seed output of the *J. standleyi* population and less variability in seed production will also mean a greater number of rare long-distance dispersal events (Augsburger and Franson 1987; Clark et al. 2001) and a greater chance of establishing a persistent remote population for *J. standleyi* than *J. chamelensis*. The dioecy to be found in both these species would exacerbate the limiting effects of low seed production on the ability of a species to 'travel' successfully, perhaps to an insurmountable extent. Like Rabinowitz (1978) we highlight the importance of differences in the dispersal phase of the life histories of common versus rare species. Unlike Rabinowitz's study, however, in this case it is the rare species which is less able to disperse widely due to its lower and more variable seed production. The divergence of conclusions between these two studies is likely to be due to the differing species characteristics and environmental milieu studied and highlight again the difficulty in identifying universal causes or markers of rarity. At least one other study using congeneric species shows evidence of an association, similar to that observed between the two species studied here, in their range size and population level seed production (Fiedler

1987). Unfortunately, other published studies of more common and rarer congeneric species (e.g., Byers and Meagher (1997)) do not provide the information necessary to make similar calculations, so that further evaluation of this hypothesis is not possible at this time.

In conclusion, our study is similar to that of other such studies of commonness and rarity in congeneric plant species, in determining more versus less reasonable possibilities rather than proposing some easily discernible cause for the observed difference in range size. Our two hypotheses of population dynamics offer differing, testable predictions that would allow discrimination of one from the other. The longevity and relatively small population size of trees will always be a major hurdle in the appropriate application of matrix population dynamics models. Nonetheless, larger sample sizes would allow analysis of sensitivity to environmental change with the capacity to reveal if one or the other species is responding differently, and might be more vulnerable, to such change (Doak and Morris 1999). Although we observe that sample sizes large enough for such an analysis may be more practicable in lower diversity, temperate zone habitats than in the high diversity of many tropical forests. Alternatively, more extensive investigation of mortality and mortality-inducing factors at the sub-canopy and pre-reproductive stages, suggested by our results to be of importance, would allow a better assessment of population replacement capacity and a more immediate return on dynamic analysis than would long-term study of the population as a whole. Of final relevance, more thorough comparison between the two species in growth and mortality of pre-reproductive individuals would not only provide better understanding of the endangered *J. chamelensis*, but also a potential management tool, a goal of central importance in the study of commonness and rarity in any forest tree.

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