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# Demographic variation in cycad populations inhabiting contrasting forest fragments

**Cristina López-Gallego**

**Abstract**   Reduced habitat quality after fragmentation can significantly affect population viability, but the effects of differing quality of the remaining habitat on population fitness are rarely evaluated. Here, I compared fragmented populations of the cycad *Zamia melanorrhachis* from habitats with different history and subject to contrasting levels of disturbance to explore potential demographic differences in populations across habitat patches that could differ in habitat quality. Secondary-forest fragments had a lower canopy cover and soil moisture than remnant-forest fragments, which may represent a harsh environment for this cycad. A smaller average plant size and lower population density in the secondary-forest fragments support the hypothesis that these fragments may be of lower quality, e.g., if plants have reduced survival and/or fecundity in these habitats. However, variation in the stage-structure of populations (i.e., the relative proportions of non-reproductive and reproductive plants) was associated with the area of the forest fragments rather than the type of habitat (remnant versus secondary forest). These results suggest that different demographic parameters may respond differently to habitat fragmentation, which may be explained if processes like adult survival and recruitment depend on different characteristics of the habitat, e.g., average light/water availability versus suitable area for plant establishment. This study shows that forest fragments may differ drastically in environmental conditions and can sustain populations that can vary in their demography. Understanding how forest fragments may represent different habitat types is relevant for evaluating population viability in a heterogeneous landscape and for designing conservation programs that account for this heterogeneity.

**Keywords**   Colombia · Cycads · Demographic variation · Habitat fragmentation · Habitat quality · *Zamia melanorrhachis*

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## Introduction

Habitat fragmentation decreases habitat size and connectivity among populations, and these habitat modifications together with the deterioration of the quality of the remaining habitat can affect population fitness within habitat patches (Andren 1994; Berglund and Jonsson 2003; Hobbs and Yates 2003). The effects of reduction in habitat size and connectivity have been extensively explored in many tropical organisms (for reviews see Laurence and Bierregaard 1997; Schelhas and Greenberg 1996), but the consequences of reduced habitat quality have received less attention. Nevertheless, plant populations in lower quality habitat patches can have small population size (Eisto et al. 2000; Vergeer et al. 2003), reduced fecundity (Angelone et al. 2007; Oostermeijer et al. 1998), and low recruitment success (Jacquemyn et al. 2003; Kery et al. 2000). In addition, habitat patches of different quality within a landscape may promote population differentiation as populations adapt to local environmental conditions (Reisch and Poschlod 2003). In fact, habitat quality may be more important than patch size and isolation in determining population distribution and turnover patterns (Fleishman et al. 2002). Consequently, exploring the viability of populations in habitat patches of differing quality may be important for prioritizing conservation efforts and for management strategies that target particular populations or population processes in fragmented forest that represent heterogeneous landscapes.

It is well known that habitat quality may affect population abundance and distribution in general (Christel et al. 2002; Lawton 1993; Schmidt and Jensen 2000; Vergeer et al. 2003). However, the effects of differing habitat quality on particular demographic attributes of plant populations are poorly know, especially for non-woody understory species in tropical forests (Bruna and Kress 2002). Habitat fragmentation and the degradation of the environmental conditions in habitat patches can affect a variety of aspects of individual fitness and be reflected in changes in population-level parameters. For example, plants in lower quality habitats could have smaller sizes, which commonly translates into reduced survival or fecundity in plant species, including cycads (Clark and Clark 1987; Vovides 1990). Changes in plant survival, growth, and recruitment can in turn alter the stage structure of populations, i.e., the relative frequency of individuals in different stages of the life cycle (Bruna and Kress 2002; Jules 1998), and overall population density (or population size) and evolutionary potential (Gram and Sork 1999). Exploring demographic parameters that may reflect the quality of available habitat and will determine population viability will provide basic information about ecological processes that are critical for population persistence, and will serve to generate hypothesis for further detailed population studies, especially in rare and endangered species where extensive demographic studies are difficult (Schemske et al. 1994).

Cycads (Cycadales: Gymnospermae) are among the most endangered groups of plants in the world (Donaldson 2003; Norstog and Nicholls 1997). Many Cycad species are facing extinction because of habitat destruction and illegal collection of wild plants for trade (Donaldson 2003; Gilbert 1984; Osborne 1995). In the New World, most cycad species are threatened by habitat loss and degradation, and many populations persist only in highly degraded landscapes (Stevenson et al. 2003). Despite the level of threat, there is scanty information about the status of populations of Neotropical Cycads in their native habitats, and about the viability of these populations in fragmented and degraded habitats. In this paper, I compare fragmented populations of the cycad *Zamia melanorrhachis* from habitats with different history and subject to contrasting levels of disturbance to explore potential demographic differences in populations across habitat patches that could differ in habitat quality. This type of information is relevant for identifying processes affecting the viability

of fragmented populations of this cycad, and for developing management strategies that can address these threats in a heterogeneous landscape.

*Zamia melanorrhachis* populations inhabit both remnant forests (i.e., forest fragments never converted to pasture) with low levels of current human disturbance, and forest fragments resulting from forest regeneration characterized by secondary-forest vegetation. Secondary-forest fragments exhibit a higher level of disturbance than remnant-forest fragments (e.g., cattle trample, log extraction, soil perturbation—but not cultivation-prior to regeneration). Secondary-forest fragments may differ in species composition and forest structure compared to the original forest habitat in these tropical ecosystems (e.g., Guariguata et al. 1997; Montgomery 2004), which in addition to current human disturbance, may result in a lower quality habitat for populations of *Z. melanorrhachis.* In contrast, remnant-forest fragments may better resemble the original forest habitat, and could potentially represent higher quality habitat for the species. To test this hypothesis, I described abiotic characteristics of forest-fragments to establish potential differences in environmental conditions among them, and compared population demographic parameters in secondary- and remnant-forest fragments: average plant size, the population stage-structure, and population density. The data suggest that secondary- and remnant-forest habitat differ considerably in environmental conditions, however population parameters are associated to different aspects of the forest fragments, and not all of them support the hypothesis that the secondary-forest habitat is of lower quality than the remnant-forest habitat for *Z. melanorrhachis* populations.

## Methods

### Study species

*Zamia melanorrhachis* is a recently described species endemic to Colombia, where it is known only from a few localities (Stevenson 2001). *Zamia melanorrhachis* is listed in the 2003 IUCN Red list of threatened plants as endangered, mainly because of severe habitat reduction (Donaldson 2003). In the Atlantic-plains region, this species is known only from one locality in the Cordoba department in Colombia. *Zamia melanorrhachis* is a small cycad with no trunk but a subterranean stem (5–8 cm in diameter) that bears 1–5 leaves (0.1–1.5 m in length), with 4–12 (rarely to 24) leaflets/leaf. As in other *Zamia* species, leaves are produced in annual flushes, but little is know about the vegetative or reproductive phenology of this species and the time required for maturity (that should be in the order of 5–10 years). Individuals are dioecious, i.e., plants produce either male cones or female cones during annual reproductive events. Male and female cones are relatively small compared to other *Zamia* species, and female cones produce *ca.* 50 seeds (1 cm in diam.), that are red in color. Seeds have no dormancy and are probably dispersed by small animals, although dispersal is usually very limited in forest cycads (Norstog and Nicholls 1997). Plants are distributed in groups of a few dozens in the understory of the forest, and very few isolated plants are observed in between groups of plants.

### Study area

This study was carried out in the Atlantic-plains region in Colombia (the exact coordinates are not given to avoid illegal extraction of wild individuals, one of the major threats for survival of Cycads populations). Almost 40 years ago this region was covered with

undisturbed forest, but deforestation in the 1960s for crop and livestock introduction resulted in almost complete destruction of forest habitats. Currently, the region is dominated by livestock pastures, some crops, and numerous small- and medium-size forest fragments (there is no continuous forest in this region). I explored most of the largest fragments in the region (fragment area > 5 ha, mostly secondary-forest fragments) and found four forest fragments containing populations of *Z. melanorrhachis*. These four forest-fragments are dispersed in an area of ~2,000 ha (Fig. 1). Fragments RF1 and RF2 are remnant-forest patches that have had no further disturbance from human activities since the time of isolation. In contrast, fragments SF3 and SF4 are the product of forest regeneration and thus have vegetation typical of secondary forests. Forest fragments have a transitional vegetation type, containing species typical from wet- and dry-tropical forests. The study zone has an elevation of 50 masl, a mean annual temperature of 27°C, and a mean annual rainfall of 2,300 mm, with two dry seasons (i.e., periods with rainfall lower than 100 mm/month) that run from December to February and from July to August. Sampling was performed during the wet season of 1998 and the dry season of the following year.

To describe habitat characteristics of the forest fragments, I calculated fragment size and shape and estimated the percentage of canopy cover and soil moisture. Fragment size and shape were obtained from aerial photographs (Fig. 1). Fragment shape was defined as the ratio between perimeter and area (P/A). The perimeter and area of the fragments were obtained using a digital planimeter (LaSico® mechanical polar planimeter, model L10, accuracy ±0.2%). The percentage of canopy cover and soil moisture were estimated at 50 points located every 10 m in two randomly placed transects of 250 m. Canopy cover was estimated using a spherical densiometer (Forestry suppliers Inc., spherical crown concave densiometer, model C). Soil moisture was estimated using a soil moisture meter (Kelway® soil acidity and moisture meter, model HB-2, accuracy ±10%). Canopy cover and soil moisture were estimated for comparative purposes and the estimates do not represent time series. Canopy cover and soil moisture were estimated during the same month (December 1998) in all fragments. Measurements were made during the beginning of the dry season, and always between 10:00 and 14:00 h, trying to reduce any biases due to cloud cover or rainfall. These two variables were arcsine transformed in order to meet normal assumptions, and compared among fragments using ANOVA and post hoc Tukey tests.

Population demographic parameters

Average plant size was estimated for each population using six size variables: petiole length, rachis length, leaflet length, leaflet width, leaflet perimeter, and leaflet area. Leaf number had little variability among plants, therefore leaf length and leaflet size variables were chosen to estimate average plant size. To estimate plant size I sampled all individuals in five 100 m² quadrats in the forest interior of each forest-fragment. Quadrats were located in randomly chosen groups of *Z. melanorrhachis* plants. Petiole and rachis length were measured in the field. Leaflet measures were obtained for the four largest leaflets in each individual. Leaflet contours were recorded on paper, and then digitalized for analysis using the program Scion Image (Rasband 2000). All size variables were highly correlated (Spearman correlation $r > 0.6$ for all pair-wise combinations), and thus they were combined to produce two overall-size factors using Principal Component Analysis (PCA). The two first principal components (PC) were then used to compare average size among populations using one-way ANOVAs and post hoc Tukey tests. The number of leaflets was used as a covariate in the analysis to exclude the effect of 'age-state' in the analysis of average plant size in the populations.
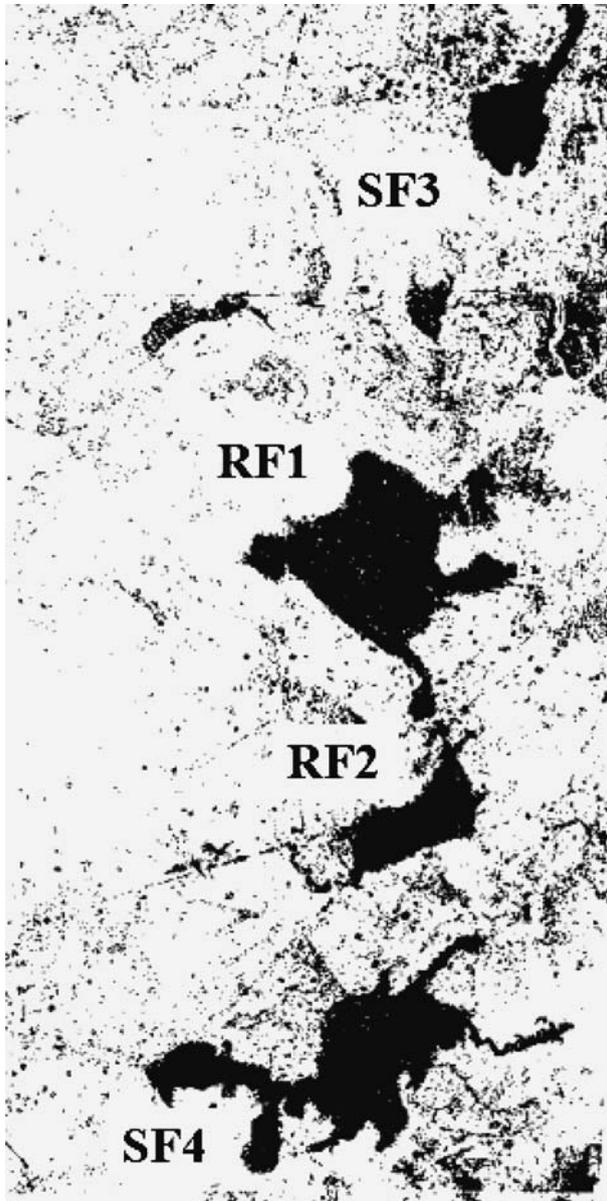
**Fig. 1** Aerial photograph of study area showing remnant-forest (*RF*) and secondary-forest (*SF*) fragments. *Scale* 1 cm² = 10 ha

The population stage distributions, i.e., relative proportions of individuals in different developmental stages in the life-cycle (Gatsuk et al. 1980), were generated using the number of leaflets as indicator of the developmental stage of individuals. The number of leaflets is a good descriptor of the demographic properties of individuals in *Zamia* species (Clark and Clark 1987; Negron-Ortiz and Breckon 1989; Negron-Ortiz et al. 1996). I recorded the

**Table 1** Habitat variables for four forest fragments (mean ± SD)

| Fragment | Area (ha) | P/A (1/km) | % Canopy cover | % Soil moisture |
|----------|-----------|------------|----------------|-----------------|
| RF1 | 31.4 | 10.8 | 89.39 ± 4.32a | 49.60 ± 24.07a |
| RF2 | 12.4 | 15.0 | 89.37 ± 3.55a | 61.40 ± 16.54a |
| SF3 | 12.8 | 11.3 | 87.25 ± 3.97b | 39.20 ± 16.52b |
| SF4 | 28.8 | 19.6 | 88.27 ± 2.77b | 36.20 ± 20.79b |

Values followed by different letters are statistically different (ANOVA, $P < 0.05$). *P/A* perimeter/area ratio

maximum number of leaflets/individual in all individuals sampled in the quadrats used to estimate average plant size. In the sampled populations, seedlings had four leaflets, and reproductive individuals had at least eight leaflets (personal observation). Using this information, I defined three major state-categories: (1) seedlings: individuals with four leaflets; (2) juveniles: individuals with six leaflets; and (3) adults: individuals with eight or more leaflets. Pair-wise comparisons of state-distributions were performed using Kolmogorov–Smirnov tests.

Finally, population density for adult individuals was estimated in each fragment using the T-square distance method (Krebs 1999). For this method, I used two 250 m long transects randomly placed in the interior of the fragment. Sample points were established each 10 m ($N = 50$ sampling points/fragment). In each point, two measurements were made: the distance from the point to the nearest plant, and the distance from this plant to its nearest conspecific neighbor outside the *T*-square angle. Distances were then used to calculate population density and its 95% confidence interval. Population density estimates were compared among populations using a one-way ANOVA and post hoc Tukey tests. All statistical tests were performed with SPSS Version 10.0 (SPSS 2003).

## Results

### Forest fragments characteristics

Fragments RF1 and SF4 had a greater size when compared to the other fragments (Fig. 1, Table 1). Forest-remnants (RF1 and RF2) had a rounded shape as indicated by a low perimeter/area ratio (P/A) (Table 1). Fragment SF3 had also a rounded shape, whereas fragment SF4 had a more elongated shape and therefore a larger forest-edge (Fig. 1). The percent of canopy cover was significantly lower in the secondary-forest fragments than in the forest-remnants (ANOVA $F_{3,220} = 2.77$, $P < 0.05$, Table 1). Likewise, the percent of soil moisture was significantly lower in the secondary-forests fragments when compared to the forest-remnants ($F_{3,220} = 14.79$, $P < 0.01$, Table 1).

### Population demographic parameters

The PCA for plant size showed that the two first components accounted for 90% of the total variance in the size variables. The first component was positively correlated to all variables, and could be considered as an indicator of overall size. The second component was negatively correlated to leaflet measures, and positively correlated to leaf length variables. Using these two PC components, comparisons of average plant size showed significant differences among populations (ANOVA for PC1: $F_{3,199} = 8.10$, $P < 0.01$; ANOVA for

**Table 2** Plant size of *Z. melanorrhachis* populations in four forest fragments (mean ± SD)

| Fragment | Leaflet length (cm) | Leaflet width (cm) | Leaflet perimeter (cm) | Leaflet area (cm²) | Petiole length (cm) | Rachis length (cm) |
|---|---|---|---|---|---|---|
| RF1 | 13.9 ± 3.2 | 3.2 ± 0.6 | 36.7 ± 7.9 | 34.7 ± 14.2 | 30.5 ± 9.9 | 9.9 ± 3.4 |
| RF2 | 15.6 ± 2.7 | 3.5 ± 0.6 | 40.5 ± 6.9 | 43.8 ± 12.2 | 35.5 ± 10.1 | 10.6 ± 5.0 |
| SF3 | 13.7 ± 3.4 | 3.1 ± 0.5 | 35.6 ± 8.2 | 33.9 ± 12.2 | 27.0 ± 11.2 | 7.4 ± 5.1 |
| SF4 | 13.3 ± 3.7 | 3.1 ± 0.7 | 34.9 ± 9.3 | 33.8 ± 15.0 | 30.4 ± 12.3 | 9.6 ± 7.8 |

All the size variables were used in a PCA. See text for statistical analyses

**Table 3** Stage-structure comparisons for *Z. melanorrhachis* populations in four forest fragments

| Fragment | RF1 | RF2 | SF3 | SF4 |
|---|---|---|---|---|
| RF1 | – | 10.31 | 25.96 | 2.90 |
| RF2 | 0.01 | – | 5.06 | 1.85 |
| SF3 | <0.01 | 0.16 | – | 13.93 |
| SF4 | 0.47 | 0.79 | <0.01 | – |

Numbers above the diagonal are $\chi^2$-values from Kolmogorov–Smirnov tests, and numbers below the diagonal are the *P*-values

PC2: $F_{3,199} = 3.72$, $P < 0.01$). The post hoc ANOVA tests for PCs show that plants from fragment RF2 have a significantly larger overall size than individuals in all other fragments, but plants in RF1 also tended to have greater size than plants in the secondary-forest fragments (Table 2).

Population state-distributions were also significantly different among populations (Table 3), but patterns did not correspond to a clear dichotomy of remnant- and secondary-forest fragments. Fragment RF1 has a very high proportion of seedlings/juveniles when compared to other fragments, except SF4 that has the highest proportion of seedlings (Fig. 2). Fragment RF2 does not differ significantly from the secondary-forest fragments, because of similar proportions of non-reproductive and adult individuals in all these fragments (Fig. 2). Fragment SF3 differs significantly from other fragments (except RF2), mostly because of a comparatively low proportion of seedlings (Fig. 2). Finally, SF4 is similar to the remnant-forest fragments because of a relatively high proportion of seedling/juveniles (Fig. 2). Populations with larger proportions of seedlings/juveniles (RF1 and SF4) were located in the forest fragments with the greatest area.

Population density for adult plants was significantly different between fragments (ANOVA $F_{3,196} = 11.01$, $P < 0.01$). Fragment RF1 had the largest value for population density, followed by fragment RF2 (Table 4), both remnant-forest fragments. The two secondary-forest fragments had a significantly lower density than the forest-remnants (Table 4), with plant density being less than half of the density in fragment RF1. The estimated population densities suggest that all forest fragments can sustain populations of at least several hundred individuals (when extrapolated to the area of the whole fragment).

## Discussion

The data showed that secondary-forest fragments have distinct habitat characteristics when compared to forest-remnants, particularly lower canopy cover and lower soil moisture.
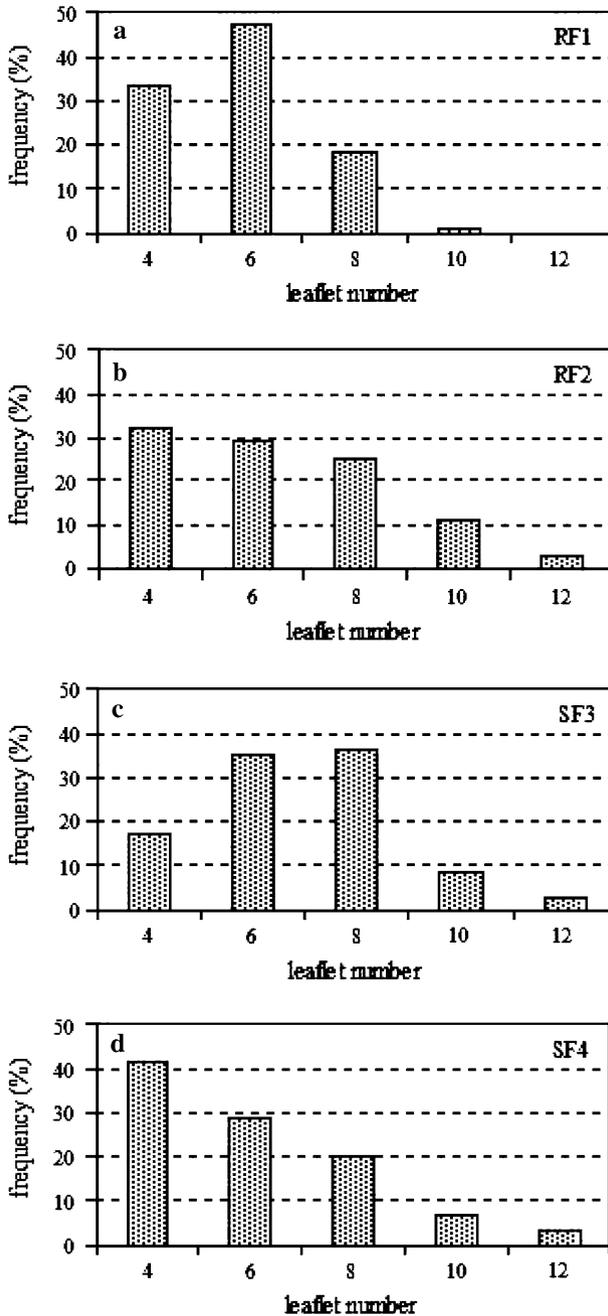
**Fig. 2** Stage-structure of four *Zamia melanorrhachis* populations based on number of leaflets for individuals (seedlings = 4 leaflets, juveniles = 6 leaflets, reproductive plants = 8–12 leaflets). See Table 3 for statistical analyses

**Table 4** Population density (individuals/100 m$^2$) of *Z. melanorrhachis* in four forest fragments and their 95% confidence intervals (*C.I.*)

| Fragment | Density | C.I. | *N* |
|---|---|---|---|
| RF1 | 8.41a | 7.02–10.39 | 197 |
| RF2 | 5.21b | 4.28–6.69 | 100 |
| SF3 | 3.68c | 3.09–4.53 | 144 |
| SF4 | 3.44c | 2.81–4.41 | 101 |

Values followed by different letters are statistically different (ANOVA, $P < 0.05$)

Population parameters like plant density and average plant size support the hypothesis that secondary-forest fragments may represent lower quality habitats and sustain populations with lower fitness, but the stage structure of populations did not show patterns congruent with the hypothesis. Therefore, even if secondary-forest fragments seem to have clear environmental differences when compared to remnant-forest fragments, it is possible that particular processes like juvenile or adult survival and recruitment respond differently to habitat changes after fragmentation and human disturbances, resulting in differing patterns for population parameters like density and stage structure. Nevertheless, sample sizes are small in this study and demographic parameters were estimated in 1 year, therefore further demographic monitoring (given than increasing sample size is not possible, as there are very few remaining populations of this endangered species) should provide insight into the relative role of ecological factors in explaining the patterns observed in this study. Below, I discuss the associations between habitat conditions and the population parameters examined in this study, and suggest hypotheses and potential avenues for future research.

All forest fragments inhabited by *Z. melanorrhachis* are large enough to contain populations of at least several hundred individuals, and their rounded shape ensures low exposure to edge effects (except for SF4). Nevertheless, there are clear differences between the secondary-forest and the remnant-forest fragments regarding canopy cover and soil moisture. Lower canopy cover and soil moisture may represent harsher environmental conditions for this type of cycad (Clark and Clark 1987; Tang 1990). Like in this study, tropical secondary-forests typically show higher levels of light availability and lower moisture than the original rainforest habitat (Gauriguata and Ostertag 2001; Montgomery and Chazdon 2001), and many studies have suggested that these kinds of environmental differences can promote changes in the physiological and morphological characteristics of plants and their life history (e.g., Everham et al. 1996; Makana and Thomas 2005; Montgomery 2004). Since there are no populations of this species in continuous forest habitat, there is no information on the spatial variation of demographic parameters prior to habitat fragmentation. Nevertheless, differences in habitat conditions between secondary- and remnant-forest fragments seem to be large compared to environmental variation in the understory of these tropical forests, and they may have a large influence in plant fitness and the demography of *Z. melanorrhachis* populations.

Reduced overall plant size, as a result of stress and reduced growth, could be the result of low habitat quality in habitat fragments (Kolb and Lindhorst 2006). In this study, plant size tended to be smaller in the secondary-forest fragments, supporting the hypothesis that the secondary-forest fragments are a low quality habitat for *Z. melanorrhachis* populations. *Zamia* species tend to produce smaller leaves in sites with higher light availability (Newell 1985), as do many other tropical forest species (e.g., Montgomery 2004), as a result of acclimation to higher light availability. Nevertheless, plants can also show reduced leaf area when exposed to water stress besides higher light availability (e.g., Noda et al. 2004).

Low soil moisture may represent a stressful condition for *Zamia* species (Negron-Ortiz et al. 1996; Tang 1990), which could negatively affect plant growth and result in smaller plants in the secondary-forest habitats. Regardless of the underlying causes, smaller plants usually have reduced fecundity in forest *Zamia* species (Clark and Clark 1987, 1988), which may result in lower recruitment in the populations in the secondary-forest fragments. In addition, smaller plants may have lower survival, which together with low recruitment could have significant negative effects on population density (and population size) and modify the stage structure of populations in the secondary-forest fragments.

If harsh environmental conditions in the secondary-forest fragments result in high seedling or adult mortality and reduced recruitment, then population density could be decreased in the lower quality habitat. The observed lower population density in the secondary-forest habitats supports this hypothesis. In other plant species, lower quality habitat has resulted in a decreasing population density because of reduced recruitment (Jacquemyn et al. 2003), or high adult mortality (Eisto et al. 2000), but estimating the relative contribution of each factor is difficult. In this study, plant density was estimated for adult individuals only, therefore a lower adult density in secondary-forest fragments might be mainly the result of higher adult mortality. However, many cohorts have reached the adult stage after habitat fragmentation, and low recruitment into the adult stage could also contribute to lower adult density. Long-term studies will be necessary to evaluate population-level differences in adult mortality and recruitment that may be responsible for variation in population density between remnant- and secondary-forest fragments. Nevertheless, information on the population stage structure could provide information on whether demographic parameters (survival, recruitment) differ consistently across habitat types and could be associated with the variation observed in population density.

The population stage-structure did not show clear patterns when comparing secondary- and remnant-forest habitats for *Z. melanorrhachis* populations. This suggests that processes resulting in decreased population density in the secondary-forest fragments may not be the same across fragments. The population stage structure was similar between populations inhabiting forest fragments of similar size, rather that between forest fragments of the same habitat type (secondary- versus remnant-forest). Populations in the fragments with the largest area have the greatest proportions of seedling and juveniles (RF1 and SF4). A higher proportion of juvenile individuals may reflect higher recruitment, but it could also result from higher adult mortality. Another possibility is that a higher proportion of juveniles resulted from adult plants shifting to smaller sizes because of stress after habitat disturbance, as shown by an understory plant in the Amazonian forest (Bruna et al. 2002), although this does not seem likely given that the population state structure was not associated with habitat type and disturbance level. A closer association of the population stage structure with habitat size rather than habitat type could indicate that the stage structure depends more on the availability of suitable habitat than on the population size (that does not correspond to habitat size, as suggested by population density). If this is true, then the differences in stage structure among populations may be the result on differing recruitment ability, rather than survival rates, as recruitment should depend more closely on the availability of suitable habitat than plant survival.

This study suggests that population parameters may respond differently to habitat fragmentation and habitat types in the remaining patches. Plant fitness may be lower in the potentially lower quality habitat of the secondary-forest fragments and this could be reflected in a lower plant density, because of high adult mortality for example. In contrast, recruitment may not be affected by habitat type, but rather by the availability of suitable habitat, that may in turn depend more on habitat area than on habitat type. Other studies

have suggested that population parameters may respond differently to habitat disturbance after forest fragmentation. For example, a study of an understory herb in an Amazonian forest showed that population parameters like density and reproductive output were not affected by forest fragmentation, but that individual responses in growth and survival resulted in altered population stage structure in forest fragments (Bruna and Kress 2002). Studies with non-tropical plants have shown that population parameters like recruitment can be affected by reduced habitat size and increased isolation but not by habitat quality (Kolb 2005), or not affected significantly by either habitat size or quality (Eckstein et al. 2004).

Population-level responses to habitat fragmentation are complex, and can vary according to the species or the species attribute analyzed (Kolb and Lindhorst 2006; Lindborg et al. 2005). Nevertheless, exploring different population parameters may provide some insight into the population processes that are mainly affected by forest fragmentation and the modification of habitat conditions. In *Z. melanorrhachis* populations the data suggest that secondary-forest fragments are a low quality habitat that negatively affects plant growth and sustains populations with lower density. However, not all population processes seem to be associated with habitat type, and processes like recruitment may depend more on the availability of germination and establishment sites rather than the average environmental conditions of the habitat type. Further studies should provide insight into the relative role of different demographic factors on explaining variation in plant fitness and population viability. This study suggests that different forest patches may vary in quality and that populations in forest fragments of different type sustain populations that can vary significantly in their demographic parameters, although not with consistent patterns for all parameters. Understanding how different forest fragments may represent contrasting habitats for populations is important for evaluating population viability in a heterogeneous landscape, which may be important for prioritizing conservation efforts or to design management strategies appropriate for populations that vary in their demography.

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