Acta Botanica Brasilica 28(4): 617-623. 2014.
doi: 10.1590/0102-33062014abb3516

Demography of the endangered tree species *Ocotea porosa* (Lauraceae) along a gradient of forest disturbance in southern Brazil

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Received: 31 January, 2014. Accepted: 23 June, 2014.

ABSTRACT

Ocotea porosa (Ness) Barroso (Lauraceae), a typical tree of the southern Atlantic Forest in Brazil, was heavily exploited for timber in the last century. With the aim of examining the status of the remaining populations, we surveyed five forest fragments in the state of Paraná, in southern Brazil, and evaluated whether disturbances caused by selective logging and fragmentation were related to population structure of *O. porosa*. We assessed demographic aspects related to tree density, size hierarchy and individual allometry, correlating those parameters with fragment structure variables (fragment size, isolation and logging level). We found that, although all populations occurred in low densities (60-440 individuals ha^{-1}), the number of adults was significantly lower in the smaller and most disturbed fragments (13 and 35 individuals ha^{-1}, respectively). We did not detect changes in allometric relationships among individuals in the five populations studied. However, we found that populations in more heavily disturbed areas presented lower size hierarchy (i.e., less dominance of larger trees) than did those in undisturbed areas, suggesting that selective logging affects the population structure of *O. porosa*, possibly affecting the rates of reproduction and fecundity, which may ultimately increase the probability of local extinction.

Key words: Size structure, size hierarchy, Araucária Forest, mixed forest, Atlantic Forest.

Introduction

High-impact selective timber extraction creates major disturbances, even causing, in extreme cases, biodiversity loss and species extinction, and is therefore considered an unsustainable activity for tropical and subtropical forests (Bawa & Seidler 1998). Logging changes habitat quality and forest structure by increasing canopy openness (and consequently light availability), destroying the undergrowth during tree removal, and modifying the soil structure because of compaction resulting from tree falls (Uhl & Vieira 1989; Bawa & Seidler 1998). In addition, selective logging can intensify the effects of forest fragmentation. For example, in fragments subjected to selective logging, tree removal creates gaps in which light intensity and ground humidity are modified, increasing the edge effects (Broadbent *et al.* 2008) and affecting several ecological processes (Laurance *et al.* 2011), including the survival of large trees (Laurance *et al.* 2000). There is therefore potential synergism between selective logging and forest fragmentation affecting ecological processes, which in turn influences the distribution and structure of plant populations (Turner *et al.* 1996; Hill & Curran 2003; Arroyo-Rodriguez *et al.* 2007).

The demographic dynamic of an exploited timber species can be variously changed by selective logging and forest fragmentation (Lobo *et al.* 2007). The main changes include tree density, which can increase or decrease after logging (Guariguata & Sáens 2002; Lobo *et al.* 2007; Arroyo-Rodríguez *et al.* 2007). The size distribution of a population, considered a synthesis of the demographic events of recruitment, mortality and individual growth rates over time (Harper 1977), can also be changed by disturbance caused by logging (Souza 2007). Calculating the size hierarchy in a population is potentially an efficient tool for measuring the effects of logging. Populations with size hierarchy are characterized by wide variations in individual sizes, relatively few large individuals contributing greatly to the population biomass, and many small ones (Weiner & Solbrig 1984). Considering that size hierarchy of plant populations varies in different habitats (Poorter *et al.* 1996; Kohira & Ninomiya 2003; Wright *et al.* 2003), and that selective logging and fragmentation modify the fragment shading characteristics, it is expected that size hierarchy and population density would decrease significantly with increasing forest disturbance (Souza 2007). Therefore, the comparison of size hierarchy among populations occurring at sites with different degrees of disturbance may reveal

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species responses to human activities (Peres *et al.* 2003; Gómez-Aparicio *et al.* 2005; Souza 2007).

In addition to demography, patterns of individual plant growth change with habitat and their competitive interactions (King 1990; Sumida *et al.* 1997; Sposito & Santos 2001) and are potentially affected by disturbance. The pattern of resources allocation in tree species for vertical or horizontal growth (height and stem diameter, respectively) are tied to different strategies of habitat occupation (Hara *et al*. 1991; Sposito & Santos 2001). For example, trees adapted to survive in shaded areas have traits that increase light interception and persistence by allocating more biomass to diameter growth than to height gain. In contrast, gap-dependent species allocate their biomass to efficient height growth and pass through the understory to reach the high-light environment of the canopy (King 1990; Gelder *et al*. 2006; Cardoso *et al.* 2010). Considering that selective logging and the effects of fragmentation can increase the light availability in the understory of a fragment, it is expected that individuals will tend to allocate more resources to growth in height than to growth in diameter.

Although the Atlantic Forest once covered a large portion of the territory of Brazil, only less than 11% of original forest remains (Ribeiro *et al*. 2009). Historically, selective logging and clearing forest for agriculture have led to high levels of fragmentation and subsequent species extinctions (Galindo-Leal & Câmara 2005). The Atlantic Forest Biome comprises rain forests, semideciduous forests, and subtropical mixed forests (Oliveira-Filho & Fontes 2000). In the state of Paraná, the subtropical mixed forests, denominated of Araucária forests, have been reduced to only 1.3% of their original area (Castella & Britez 2004). *Ocotea porosa* (Ness) Barroso (Lauraceae) is a large tree (> 20 m in height) once widely distributed in Araucária Forests in southern and southeastern Brazil. The dense wood of *O. porosa* is highly appreciated for wooden furniture and other wooden items (Carvalho 2003). The species became rare due to intensive logging in the last century (Varty & Guadagnin 1998) and is therefore categorized as a vulnerable species by the International Union for Conservation of Nature (IUCN 2013).

In this study, we assessed the demographic atributes of five populations of *Ocotea porosa* occurring in a gradient of logging, fragment size and connectivity in southern Brazil. We sought to determine whether size structures (the distribution of individual by height and diameter) differ among populations in the gradient; whether fragment size, forest canopy coverage and stem density (surrogates of disturbance level) affect density and size structure of *O. porosa* populations; and whether there are variations in the allometry (relationship between diameter and height) of individuals along the gradient. Finally, we used demographic atributes to discuss the conservation status of local populations and to assist in the management of *O. porosa*.

Methods

Study area

The study was carried out in the state of Paraná, southern Brazil, in areas of occurrence of Araucária Forests. This type of forest, also known as Mixed Ombrophylous Forest, was once distributed throughout the south and southeast of Brazil, as well as across eastern Paraguay and northern Argentina (Fiaschi & Pirani 2009). This subtropical rain forest is dominated by the endemic Gymnospermae species *Araucaria angustifolia* (Bertol.) Kuntz and lies in a transition zone between tropical and temperate climates, with well distributed rainfall throughout the year and moderate temperatures (Maack 2002). Because these forests are located in an ecotone, they show particular features, including mixed tropical and temperate flora elements.

We systematically traversed the occurrence areas of Araucária Forest in southern, eastern and southeastern Paraná to find populations of *Ocotea porosa*. We searched for *O. porosa* in 10 fragments. These fragments were generally small (< 100 ha) and presented signs of disturbance from logging. Apparently, *O. porosa* had disappeared from most of them, possibly because of the intense timber extraction (Backes & Irgang 2002). We selected five of those fragments on the basis of the presence of adult *O. porosa* trees. Two of the fragments (areas 1-SJT and 3-SJT) are located in the municipality of São João do Triunfo (25°37’03”S; 50°21’40”W and 25°41’23”S; 50°09’47” W, respectively), one (area 2-CUR) is located in Curitiba (25°26’11”S; 49°13’10”W), and two (areas 4-FPI and 5-FPI) are located in Fernandes Pinheiro (25°22’23”S; 50°09’47”W and 25°22’54”S; 50°35’00”W, respectively). Although all of the study sites are currently protected areas, they were all disturbed by selective logging of *O. porosa* and other wood species in the past 50 years. The regional climate is classified as Köppen-Geiger type Cfb, characterized by warm summers and cool winters, with a relatively narrow annual temperature range, precipitation evenly dispersed throughout the year, and no dry season (Kottek *et al*. 2006). In Paraná, Araucária Forests occur in regions with average temperatures ranging from 18°C to 22°C, more than five nights of frost per year and mean annual rainfall of 2000 mm (Maack 2002). Elevations range from 815 m and 902 m.

The five areas were chosen to represent a range of fragments varying with respect to nearest neighbor distance and size, fragment area and historical logging levels (Tab. 1). The distance and size of the nearest neighbor, as well as the area of the fragment, were measured in ArcGis (http://www.esri.com/software/arcgis) with images from Google Earth. The degree of disturbance by logging was inferred *a priori* by field incursions and by measuring the percent canopy openness, with a spherical crown densiometer (Forestry Suppliers, Jackson, MS, USA) in the center of each 10 × 10 m grid (see the section *Data collection and analysis*). We

Table 1. Characteristics of the five fragments studied in the state of Paraná, in southern Brazil.

Site	1-SJT	2-CUR	3-SJT	4-FPI	5-FPI
Fragment area (ha)	18.0	3.9	31.5	27.0	649.0
Nearest neighbor distance (m)	450	1,532	25	25	25
Nearest neighbor area (ha)	61.0	1.6	9.6	83.0	83.0
Logging level	high	low	low	intermediate	low
% canopy openness (mean±SD)	33.5±15.9	4.8±2.8	2.5±1.73	10.6±6.3	4.0±2.1
Stems (DBH>5cm) per ha (mean±SD)	15.0±10.9	85.0±79.9	95.7±27.3	78.5±35.1	109.25±94.1

also calculated the density of all stems with a diameter at breast height (DBH) ≥ 5 cm in each quadrat, as an indirect measure of past logging (Tab. 1). Thus, the five areas were classified according to the level of disturbance, as follows:

- High disturbance—signs of intense human activity and management of understory, high frequency of gaps with significant canopy openness (≥ 30% opening), low stem density (≤ 20 stems ha^{-1}), and prevalence of herbaceous and shrub species in the understory;
- Intermediate disturbance—signs of moderate human activity, high frequency of gaps with intermediate canopy openness (10-30%), intermediate stem density (20-80 stems ha^{-1}), and high density of shrub species in the understory;
- Low disturbance—little evidence of human interference, a relatively closed canopy (openness ≤ 10%), high stem density (≥ 80 stems ha^{-1}), and presence of more than two strata.

Although the areas showed a mixture of characteristics, implying different levels of habitat disturbance, area 1-SJT can be considered the most disturbed area, because it comprises a forest with open canopy and where economically important woody species are rare compared with the other areas, whereas area 5-FPI can be considered the most preserved (Tab. 1). Areas 3-SJT and 4-FPI showed intermediate disturbance. Area 2-CUR presumably suffers a strong edge effect (because it is an urban fragment and is very small).

Data collection and analysis

In each of the five fragments, we delineated a 40 × 50 m plot (2000 m^2) divided into a grid of 10 × 10 m quadrats (n = 20). We established each plot at a minimum distance of 20 m from the edge of fragments to minimize the edge effect. All individuals of *Ocotea porosa* within the plot were marked and measured in height and stem base diameter at soil level (BD).

In each area we calculated the density of individuals of *Ocotea porosa* and estimated the density in 1 ha. To test whether density (the dependent variable) correlated with the fragment size, percent canopy openness and density of forest stems with DBH ≥ 5 cm (the independent variables), we used adjusted logarithmic and linear regressions.

For a comparative analysis of the size structure (height and BD) among populations we calculated the Gini coefficient (*G*) using the program WINGINI, version 1.0 (Santos 1996). The *G* measures the difference in size structure (hierarchy, based on height and BD) of individuals in the population and ranges from zero to one (Weiner & Solbrig 1984): values close to zero indicate less difference among individuals (or low size ranking); and values close to one indicate greater inequality of size (or high size ranking). The variance in *G* was generated by bootstrap resampling with 1000 replicates, also with WINGINI, version 1.0. The resulting *Gm* (*G* mean) and its standard error express the variation in *G* within the sample (Weiner & Solbrig 1984); the absence of overlapping in standard error bars demonstrates statistical differences. To visualize the degree of "unequal size" among the populations, we built Lorenz curves (Weiner & Solbrig 1984). The Lorenz curve shows the cumulative percentage of the population against the cumulative percentage of plant height or BD. The concept of inequality expressed by the Lorenz curve is fundamentally different and represents an alternative to the concept of variation of symmetry used for distribution in classes of size (Damgaard & Weiner 2000).

To infer the allometric relationships of individuals along the disturbance gradient, we used height (x) and BD (y) data. We used the equation $y = \gamma. x\beta$, converted into a linear equation after logarithmic transformation ($\log \gamma = + \beta \log x$). For the regressions, we used the standardized major axis (SMA) method, which is considered the most suitable method for such allometric relationships because it reduces the standard error of the slope (Warton *et al.* 2006). To calculate the differences of β and γ, we used the software SMATR, version 2.0 (Falster *et al.* 2006), following Warton *et al.* (2006). The software follows a sequence equivalent to ANCOVA for linear regressions but with algorithms adapted to the SMA method. This analysis is to determine whether the slopes of the lines (β) are equal, as well as whether the relationship between x and y is the same among the different samples. We considered $\alpha = 0.05$ in all analyses.

Results

Demography

A total of 219 individuals of *Ocotea porosa* were sampled in the five fragments under study. In the densest fragment (area 2-CUR), the estimated population density was 440 individuals ha^{-1}, approximately seven times greater than the 60 individuals ha^{-1} estimated for the fragment with the lowest density (area 1-SJT). In the three remaining fragments (areas 3-SJT, 4-FPI and 5-FPI), the estimated population density was intermediate (115 individuals ha^{-1}, 215 individuals ha^{-1} and 265 individuals ha^{-1}, respectively). We found that the mean density of *O. porosa* did not correlate with fragment size ($r^2=0.02$, $p>0.05$), canopy openness ($r^2=0.62$, $p>0.05$) or density of stems with a DBH > 5 cm ($r^2=0.37$, $p>0.05$). Of the 219 individuals sampled, only 13% had a BD ≥ 5 cm, representing the proportion of adults. In the five populations (1-SJT, 2-CUR, 3-SJT, 4-FPI and 5-FPI), these proportions were 58%, 3%, 13%, 4% and 28%, respectively.

The hierarchy in height and BD distributions, measured by determining the mean *G* (*Gm*), differed among populations (Fig. 1). Considering height distributions, populations in the areas 3-SJT and 5-FPI were highly hierarchical (higher *Gm*), followed by the populations of the other three fragments (Fig. 1A). The *Gm* also indicated hierarchy in the BD distribution, with lower values in area 1-SJT and higher values in areas 3-SJT and 5-FPI (Fig. 1B).

The Lorenz curves indicated that there were size inequalities (size distributions differed from the absolute equality line) in all of the *Ocotea porosa* populations studied (Fig. 2). Regarding height, it was possible to observe that for a same proportion of 85% of individuals (Fig. 2A), the populations in areas 3-SJT and 5-FPI had much less accumulated height (≈12%) than did those in areas 1-SJT (65%), 2-CUR (55%) and 4-FPI (43%). This indicates that 3-SJT and 5-FPI populations have higher size hierarchy, i.e., they have a large number of small individuals and a small number of large trees. Regarding BD, the Lorenz curve for area 1-SJT showed that 85% of individuals accounted for 63% of the accumulated BD, whereas in the other areas these proportions were much lower (< 20% of accumulated BD), indicating that the size hierarchy was lower in the 1-SJT population than in the others (Fig. 2B).

Allometric relationships

Height explained a large proportion of the plant diameter variation in the five populations studied (high r^2 values), especially in areas 1-SJT, 5-FPI and 3-SJT, where r^2 values were approximately 0.90 (Tab. 2). The populations of areas 2-CUR and 4-FPI showed greater variation in individual forms, with r^2 values much smaller those observed for the other populations. All populations of *Ocotea porosa* studied showed regression lines with the same slopes (β), i.e. the same relationship between the variables BD and height (Tab. 2).

Discussion

The study of five populations of *Ocotea porosa* in a gradient of disturbance in the state of Paraná showed that, in general, populations of the species occur in low densities (60-440 individuals ha^{-1}), possibly reflecting the impact of selective logging in the region. We also observed that *O. porosa* populations presented lower size hierarchy (i.e., less dominance of larger trees) in the more disturbed areas than in the undisturbed areas, suggesting that logging and fragmentation affect the structure of this species, possibly impacting the rates of reproduction and fecundity, which could lead to local extinction (Turner *et al.* 1996; Arroyo-Rodríguez *et al.* 2007).

The low density of *Ocotea porosa* in the study area as a whole (mean, 219 individuals ha^{-1}) is even lower if we considered only the adults (30 individuals ha^{-1}, or 13% of the total abundance). Two previous studies conducted in Brazil found small and large populations of *O. porosa* (39.5 and 443 individuals ha^{-1}, respectively) in protected and minimally disturbed areas of the state of Santa Catarina (Caldato *et al*. 1999; Bittencourt 2007). Therefore, *O. porosa* can apparently occur in very small populations, even in the absence of perceptible human perturbations. However, along the gradient studied, *O. porosa* populations were more severely reduced when occurring in areas where logging had had a high impact. For example, in area 1-SJT, characterized as a fragment highly affected by logging, the density was only 60 individuals ha^{-1}, suggesting that disturbance had affected the population size. In contrast, the densest population (440 individuals ha^{-1}) was found in a fragment that was quite small (area 2-CUR) but had a history of relatively low logging intensity. A larger fragment, which was also the least disturbed (area 5-FPI), was also characterized by a dense population (265 individuals ha^{-1}), whereas the other medium-sized fragments, where the impact of logging was low to intermediate (areas 3-SJT and 4-FPI), had intermediate population densities. Therefore, although we did not capture the direct effects of disturbance on population size in our gradient (population density not being found to correlate with fragment size, canopy cover or forest density), we have provided indirect evidence that populations of *O. porosa* can be reduced in heavily logged areas.

There were marked differences in size hierarchy between the most disturbed fragment (area 1-SJT) and the most preserved areas (areas 3-SJT and 5-FPI) which were consistent with *G* values and Lorenz curves for height and BD distribution. In other words, areas that had been more intensively logged had populations with less inequality in size structure, which can be interpreted as a direct effect of the removal of adult trees. These results are supported by those of previous studies in which increased differences in

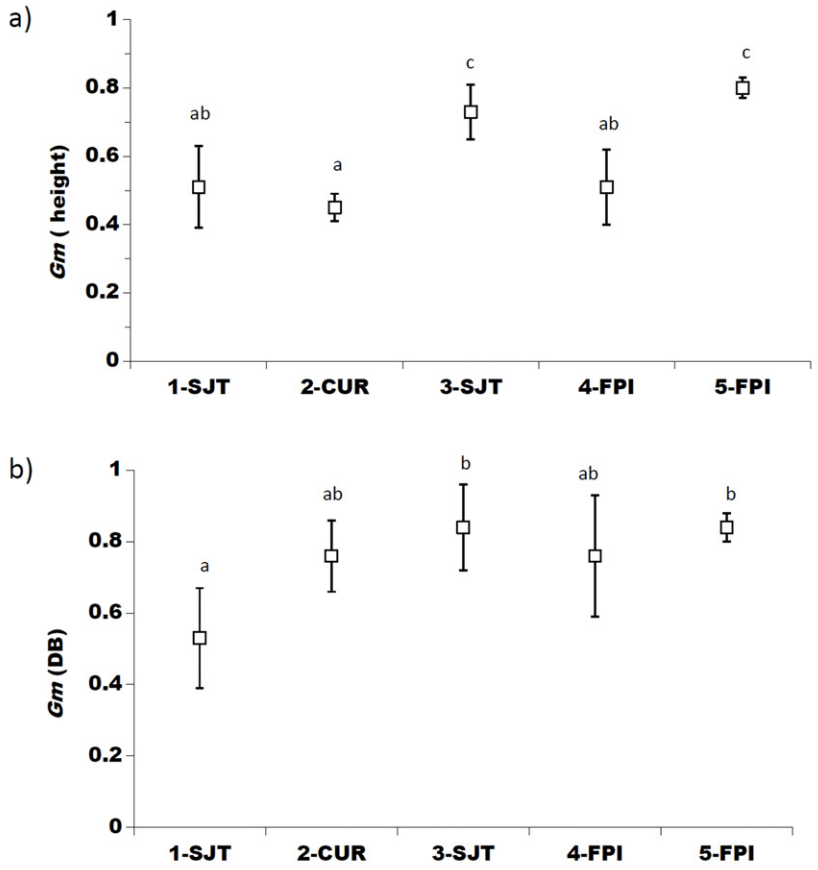

Figure 1. The mean Gini coefficient (*Gm*±SD) for height (A) and stem base diameter at soil level (B) in five populations of *Ocotea porosa* in southern Brazil. Means followed by the same letter do not differ statistically (p>0.05).

Table 2. Parameters of the regression analysis between stem base diameter at soil level (log) and plant height (log) in five populations of *Ocotea porosa* in southern Brazil.
Means followed by the same letter do not differ statistically (p>0.05).

Area	Slope (β)	r^2	N
1-SJT	1.04±0.10^{a}	0.98	12
2-CUR	1.08±0.15^{a}	0.54	88
3-SJT	1.14±0.17^{a}	0.88	23
4-FPI	1.21±0.22^{a}	0.61	43
5-FPI	0.97±0.08^{a}	0.92	45

size among individuals of tree species were positively associated with the time since logging last occurred (Ludqvist 2004; Rouvinen & Kuuluvainen 2005). In addition, the lower size differences among individuals in disturbed populations reveal possible limitations for seed production, seed dispersal and germination, potentially affecting seedling establishment and recruitment (Harper 1977). For example, *Ocotea porosa* has been shown to be self-compatible and in some areas to depend on a very small insects (thrips, Frankliniella gardeniae: Thysanoptera) for pollination, resulting in a low (10%) rate of fruit formation (Danieli-Silva & Varassin 2013). The short distances reportedly achieved by thrips in flight and the small population density of *O. porosa* could together reduce the chances of cross-pollination for this species, reducing the seed formation, seedling establishment, and resulting in low size hierarchy. Furthermore, although fruits of *O. porosa* are dispersed by generalist, abundant bird species and relatively high (60%) germination rates have been reported (Carvalho 2003), the decreasing number of reproductive adults could affect seed formation and the number of seedlings, thus affecting size hierarchy.

In addition to problems in reproduction and seed formation, the lower size hierarchy in populations of the most disturbed areas (in comparison with the more preserved areas) may be an indirect effect of canopy openness. Although *Ocotea porosa* is a shade-tolerant species in its first years of life (until reaching approximately 1 m in height), it depends on gap openings in order to grow and establish itself in the community (Inoue *et al.* 1984). As a result, a cohort composed of juveniles (1-2 m in height) may be present in these disturbed areas (C. A. Munhoz, pers. obs.), resulting in less hierarchical populations.

The allometric relationship between BD and height showed that individuals among populations of *Ocotea porosa* did not differ in their growth rate (inferred by the

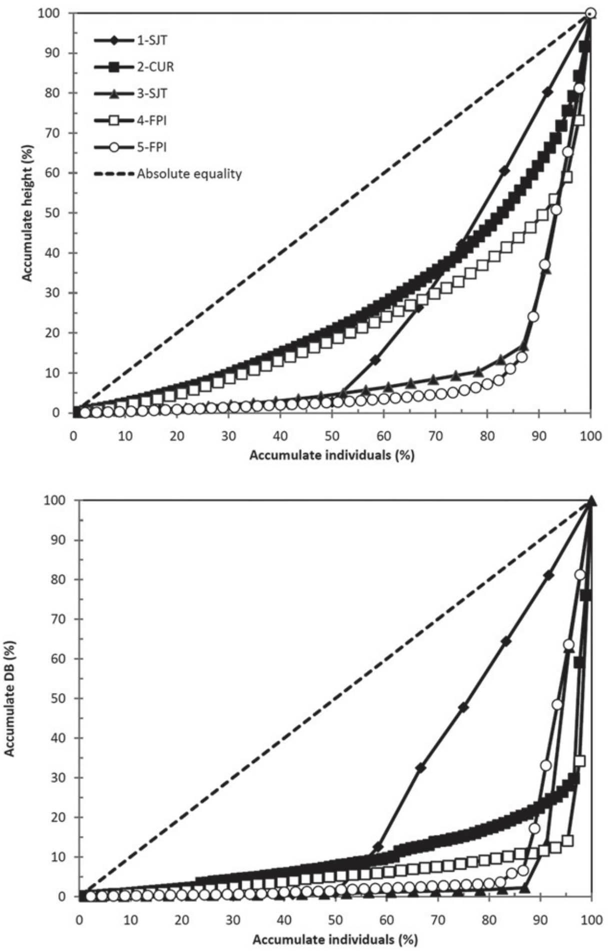

Figure 2. Lorenz curves for height (A) and stem base diameter at soil level (B) in populations of *Ocotea porosa* in five forest fragments in southern Brazil.

slopes). However, the models of the relationships between height and BD were less adjusted for individuals in areas 2-CUR and 4-FPI (lower r^2 values). The individuals in those areas showed higher slenderness (i.e., a smaller diameter than expected for a given height). Competitive interactions affect the morphology of plants (Ellison & Rabinowitz 1989; Geber 1989), and one can assume that the denser population in area 2-CUR and the higher stem density in areas 3-SJT and 5-FPI could result in higher intraspecific or interspecific competition, affecting plant slenderness. Nevertheless, no direct evidence was found, suggesting that allometric relationships may result from other factors not considered in the present study.

Ocotea porosa, once one of the dominant species in Araucária Forest, has been indicated as a species vulnerable to extinction (Varty & Guadagnin 1998), especially resulting from Araucária Forest fragmentation in the state of Paraná (Castella & Britez 2004). Recent studies have consistently demonstrated that isolated populations suffer high levels of endogamy (Bittencourt 2007) and highly limited reproduction (Danieli-Silva & Varassin 2013). Our study adds more drama to this novel: we found that natural populations are very rare and strongly uncharacterized (by low densities and low size hierarchy) in some regions. In addition to the fragmentation of Araucária Forests, the disturbance caused by logging seems to severely interfere with the population structure. Furthermore, conservation initiatives for *O. porosa* must consider this alarming situation of natural populations and reverse the trend toward low densities found in some of the protected areas studied.

Acknowledgments

We are grateful to Valderês A. Souza, for facilitating the study; to Victor Zwiener, José A. Pimenta, Adelar Mantovani and the two anonymous referees, for their suggestions to improve the manuscript, and to the Brazilian *Instituto Chico Mendes de Conservação da Biodiversidade* (ICMBio, Chico Mendes Institute for Biodiversity Conservation) for issuing the necessary permits for the fieldwork in Irati National Forest. This study received financial support from the *Empresa Brasileira de Pesquisa Agropecuária* (Embrapa, Brazilian Agency for Agricultural Research; research grant for the project "Conservation of threatened species of Mixed Ombrophilous Forest" and scholarship grant to JVS) and the Brazilian *Conselho Nacional de Desenvolvimento Científico e Tecnológico* (CNPq, National Council for Scientific and Technological Development; Research Productivity Grant no. 304650/2012-9 to MCMM).

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