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ORIGINAL PAPER

Rock outcrops reduce temperature-induced stress for tropical conifer by decoupling regional climate in the semiarid environment

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Abstract We aimed to understand the effect of rock outcrops on the growth of *Podocarpus lambertii* within a microrefuge. Our hypothesis holds that the growth and survival of this species depend on the regional climate decoupling provided by rock outcrops. To test this hypothesis, we characterized the microclimate of (1) surrounding vegetation, (2) rock outcrop corridors, and (3) adjacencies. We assessed population structure by collecting data of specimen stem diameter and height. We also assessed differences between vegetation associated or not with outcrops using satellite imaging. For dendrochronological analyses, we sampled 42 individuals. Tree rings of 31 individuals were dated, and climate-growth relationships were tested. Rock outcrops produce a favorable microclimate by reducing average temperature by 4.9 °C and increasing average air humidity by 12 %. They also reduce the variability of atmospheric temperature by 42 % and air humidity by 20 % supporting a vegetation with higher leaf area index. Within this vegetation, specimen height was strongly constrained by the outcrop height. Although temperature and precipitation modulate this species growth, temperature-induced stress is the key limiting growth factor for this population of *P. lambertii*. We conclude that this species growth and survival depend on the presence of rock outcrops. These topography elements decouple regional climate in a favorable way for this species growth. However, these benefits are restricted to the areas sheltered by rock outcrops. Although this microrefuge supported *P. lambertii* growth so far, it is unclear whether this protection would be sufficient to withstand the stress of future climate changes.

Keywords Microrefugia · Tree ring · Microclimate · *Podocarpus lambertii* · Tropical dendrochronology · Climate change

Introduction

Climate is the main abiotic factor that regulates species distribution (Lomolino et al. 2010), and its variability depends on different spatial scales, according to a hierarchical structure. The macroclimate refers to the variability at the continental scale (>100 km), the mesoclimate refers to the regional variability (>1 km), and the local climate refers to the variability dependent on local elements of the topography (<1 km), while the microclimate refers to the variability at the finest scale (<100 m) (Geiger et al. 2009). Although, species distribution is mainly defined by macroclimatic and mesoclimatic conditions in the main distribution area, some populations may be found outside of this area in specific sites that provide more favorable microclimatic conditions in an otherwise hostile condition (Hylander et al. 2015).

For instance, elements of the topography, like mountains and deep valleys, as well as the rock outcrops, can reduce the effects of in situ climatic conditions, permitting the growth and survival of plants that would otherwise decline in the present macroclimate and mesoclimate (Austin and Niel 2011; Dobrowski 2011; Keppel et al. 2012). They are like outliers in the gradients of abiotic variables that influence species distribution. These populations are usually reminiscent of long histories in the contraction and expansion of species distribution (Rull 2009; Hampe and Jump 2011).

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These areas with favorable in situ conditions played an important role in species survival during glacial and interglacial climate changes and continue to influence plant life through the present day. Such areas are termed microrefugia, which allow small populations to survive away from their main distribution (Rull 2009). During glacial stages, microrefugia were related to warmer conditions that supported thermophilous species. In the course of interglacial periods, they provided cooler environments for cold-adapted species (Dobrowski 2011; Mee and Moore 2013). Usually, populations inhabiting these microrefugia are from a subset of species that retain traits allowing their survival within the confines of those singular sites (Mee and Moore 2013). These singular sites provide insight into species dynamics and the ecological stresses that affect them, in particular due to climate changes (Hampe and Jump 2011).

In Brazil, *Podocarpus lambertii* Klotzsch ex Endl. is usually associated with cool and wet climates from relatively higher southern latitudes (Ledru et al. 2001). This species used to have a broader distribution across the country during the end of the Last Glacial Maximum (LGM) when northern areas had a cooler and wetter climate. Nowadays, it has a continuous distribution in southern and southeastern areas of Brazil and a discontinuous distribution in lower latitudes of northeastern Brazil (Ledru et al. 2007). In the northernmost area, a population is found in a semiarid region, and it grows within corridors and adjacencies of rock outcrops. In previous research, we have shown that individuals of this population are able to jointly regulate stomatal distribution in leaves and dimension of stem tracheids in order to survive in this extreme habitat (Locosselli and Ceccantini 2012). However, we believe that anatomical plasticity is not enough to explain how this population is able to withstand the extremes of this habitat. Somehow, the presence of the rock outcrops seems to benefit the growth of these individuals.

In order to understand the positive impact of microrefugia, one must identify the climate factors that limit species development within that singular site. The use of dendrochronological methods can provide precise information that helps us to understand how climate variables modulate tree growth (Fritts 1976). Previous research successfully analyzed such limiting climatic factors on tree growth. Frequently, species distribution limits were studied on the basis of altitudinal (e.g., Morales et al. 2004; Dang et al. 2013; King et al. 2013) and latitudinal gradients (e.g., Carrer et al. 2010; Hart et al. 2010; Herrero et al. 2013).

The aim of this study is to understand the role of rock outcrops on the growth of a *P. lambertii* population within the semiarid northernmost limits of its distribution. Our hypothesis holds that the growth and survival of this population depend on decoupling from the regional climate provided by rock outcrops. We further investigated temperature as a factor limiting growth and the resilience of these *P. lambertii* individuals inhabiting the corridors and adjacencies of rock outcrops.

Material and methods

Species and sampling site

We sampled individuals of *P. lambertii* from a population at its northernmost distribution limit (11° 12′ 24″ S–41° 35′ 25″ W, 1280 m), as shown in Fig. 1a. The area is located in Morro do Chapéu Municipality (Bahia State). Plotted sites represent 467 herbaria and wood collection records from 35 institutions obtained at speciesLink (CRIA) (Fig. 1a). Climate of this area has a mean temperature of 20.2 °C and annual precipitation of 694 mm year^{-1} (Instituto Nacional de Meteorologia, INMET, 1913–2012). The growth season usually occurs between October and May in that site when monthly precipitation is higher than 60 mm (Worbes 1999).

The sampling site was a hilltop with several rock outcrops distributed in an area of approximately 15 ha. The height of these rock outcrops ranged from 0.6 to 15 m, and their distribution formed continuous corridors along this area. In order to characterize that site, three categories of microenvironments were defined (Fig. 1d): (i) the transitional surrounding vegetation matrix between Caatinga and Cerrado formations, both types having xerophytic and heliophytic species (Rizzini 1997), and the areas inhabited by *P. lambertii*, (ii) adjacencies having rock outcrops on one side only (Fig. 1b), and (iii) corridors formed by two or more rock outcrops (Fig. 1c).

Microclimatic monitoring

To understand the impact of rock outcrops on microclimate, we installed 15 data loggers (U23 HOBO ONSET) for temperature and air relative humidity measurements during 96 h at the beginning of January 2013. These 96 h comprised a sunny day with clear sky, a sunny day with sparse clouds, and two cloudy days, with a short light rain in the last one. Three of these data loggers were placed over the rock outcrops at about 1.5 m above the rock surface to characterize the atmospheric temperature and the relative humidity variability. Additional five data loggers were placed in the corridors, five were placed in the adjacencies, and two were installed in the surrounding vegetation at 150 and 300 m from the nearest rock outcrop at the western side of the hill. The 10-min average values by site categories were calculated to represent a 24-h period. The resulting values were plotted, and the temperature and relative humidity differences were tested during the three most physiologically demanding hours of the day: 1100, 1200, and 1300 hours. Differences were tested using the Kruskal-Wallis test and a nonparametric multiple-comparison test from the "pgirmes" package (Giraudoux 2011).

With this design, we aimed to understand solely the microclimatic differences among these three microenvironments and how they relate to the atmospheric measurements during the middle of the rainy season, and likely, the middle of the growth period for this species. We did not intend to evaluate

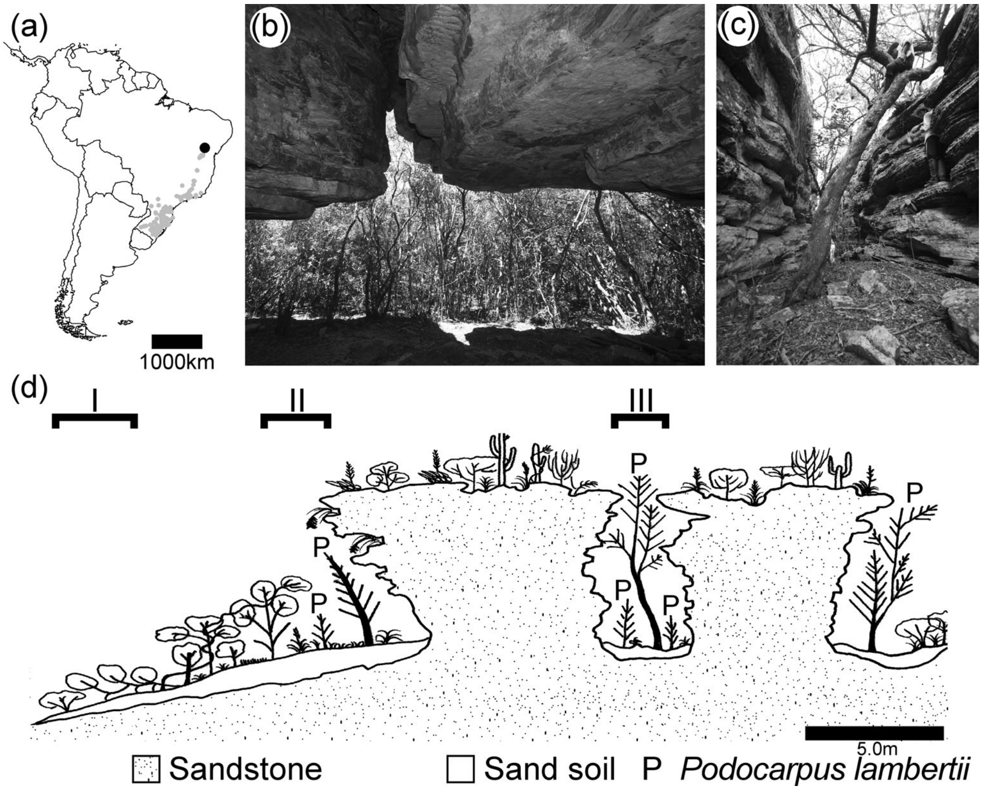

Fig. 1 Sampling site. **a** Distribution of *P. lambertii* based on herbaria records (*gray*) and the study area (*black*). **b** Example of area in the adjacency category, with the rock outcrop shelter on one side (*in the back*). **c** Photo of one of the biggest *P. lambertii* specimens. It was found growing in a rock outcrops corridor. **d** Sketch of sampling site showing the three environmental categories: (i) surrounding vegetation, (ii) adjacency, and (iii) corridors. *Podocarpus lambertii* specimens are indicated by the letter *P*

seasonal and interannual differences among them. It is also important to note that temperature and relative humidity data is not under the influence of the previous long dry season as it took place a few months after it, during the rainy period.

To further understand how the presence of the rock outcrops decouples the atmospheric temperature and relative humidity, we built linear regressions between the three microenvironments and the atmosphere microclimatic variables. Differences among the linear fits were tested using analysis of covariance (ANCOVA) and a post hoc test with the “lsmeans” package (Lenth and Herve 2015). We used these analyses to test if the slope values of the linear fits are significantly different or not among the three microenvironments. Slope values closer to 1.0 indicate that the measured microclimate data variability is similar to the atmospheric climate, while values smaller than 1.0 indicate the evidence of decoupling by reducing the microclimate variability.

Remote sensing

Remote sensing techniques were used to collect data about *P. lambertii* growth area in the study site and differences in vegetation types. High-resolution panchromatic (0.5 m of resolution) and multispectral (2 m of resolution) images from the Pléides Satellite (Astrium-CNES, August 2012) were used in these analyses. Normalized Difference Vegetation Index (NDVI) was calculated using red and infrared images. Afterward, the Leaf Area Index (LAI) was calculated based on the NDVI values (Zhu et al. 2013). LAI represents the one-sided green leaf area per ground surface area unit in broadleaf canopies. With the resulting image, classes of nonvegetated areas (lower values of LAI) and vegetation types (small, medium, and higher values of LAI) were created. All specimens were plotted in the LAI class image. Living and dead individuals were plotted using different colors. Analyses were performed using IDRISI Selva software (Clark Labs).

Population structure

In that hill top, we actively searched in about 40 % of that area for all individuals of this species, from seedlings to mature trees, and obtained values of stem diameter, plant height, and height of the closest rock outcrop. This resulted in a dataset of 135 specimens that was used to understand this small population structure and the influence of rock outcrops on the maximum dimensions of trees growing in this microrefuge. Population structure was analyzed by histogram graphics, and the relationship between tree size and rock outcrop height was tested by linear fit. For the former analyses, we used only the individuals with height equal to, or higher than, 90 % of the height of the closest outcrop. By doing so, we could test whether *P. lambertii* maximum height was constrained by the height of the closest rock outcrop. All previous analyses were performed using R software (R Core Team 2013). The geographical positions of all individuals were recorded in the field.

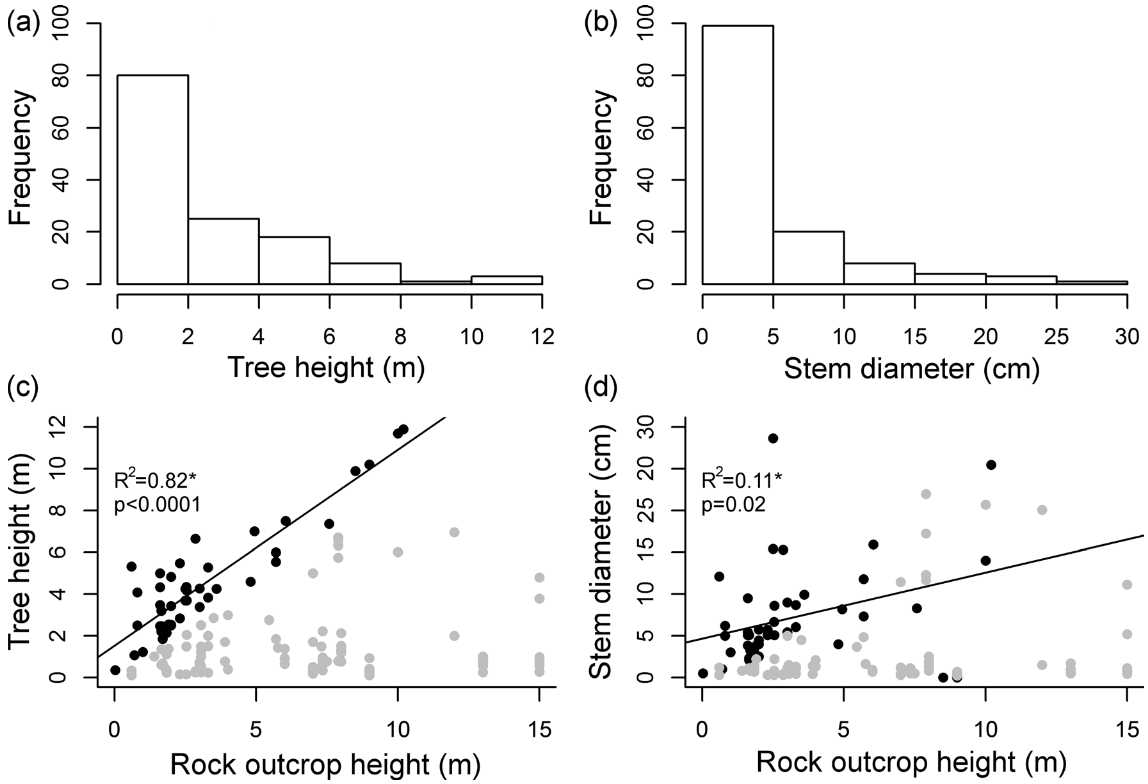

Fig. 2 Population structure of *P. lambertii* and the influence of the nearest rock outcrop height on tree size. **a** histogram of specimen height, **b** histogram of specimen stem diameter, **c** linear fit between trees and rock outcrops height, where trees with at least 90 % of the rock outcrop height (black) are plotted together with all other individuals (gray), and **d** linear fit between the stem diameter of the same individuals plotted in **c** and rock outcrop height. Asterisk indicates statistically significant for p value smaller than 0.05

It is important to highlight that the population structure fieldwork was performed after an unusually long dry season. During data acquisition, several dead individuals were found. Additionally, many living individuals had heavily damaged crowns with a high proportion of dry leaves in their crown. Based on our long experience in that site, we have never seen such a high number of damaged and dead *P. lambertii* trees. The geographical positions of those individuals were also recorded and plotted.

Tree growth analysis

We sampled stem discs and increment cores of 43 individuals of *P. lambertii* in February of 2004, February of 2009, and January of 2013. All trees were growing in the aforementioned conditions. Two to four cores were obtained for all individuals using an increment borer (5 mm). All samples were left to dry and were polished using sandpaper. Tree rings were marked and counted under stereomicroscope and then measured using the Lintab 6 system (Rinntech, Heidelberg, Germany). The dating process was done using TSAP-Win software (Rinntech, Heidelberg, Germany), and it was verified using COFECHA software (Holmes 1983). We started dating cores from the same tree and later from different trees. The final residual chronology was built using Arstan software (Cook and Kairiukstis 1990; Cook and Holmes 1996), in which linear regression and negative exponential functions were used to de-trend each dated radius. The expressed population signal (EPS) was calculated in 30-year segments to verify if the growth signal was well represented by the number of samples in each segment (Wigley et al. 1984).

With the resulting residual chronology, the correlations between climate variables and growth residuals were performed. Climate data were provided by INMET (National Institute for Meteorology) from a climate station located in the same municipality as the sampling site. The following monthly variables were used: cloud cover, number of hours of sun, days of precipitation, precipitation, and maximum temperature. Although the climate station was first installed in 1913, there are several gaps in the time series, and those gaps are different among all climatic variables. To address this problem, we decided to show the length of time series for each variable used in all correlations. In order to test if climatic variables had additive effects on tree growth or if they were collinear, we built three climate/growth linear models. For that purpose, we used temperature and precipitation, which are the variables with the longest time series. We built two models for each one of the variables and a third with the influence of both temperature and precipitation. All three models respect the assumptions of normality of response variable and residuals, and residual homoscedasticity. We chose the best linear model based on Akaike's information criterion (AIC). Two models are considered different if the AIC value is higher than two, and the best model is the one with the smallest AIC value (Faraway 2005). All analyses were performed using R software (R Core Team 2013).

Results

Microclimate

The presence of rock outcrops decouples microclimate from atmosphere climate in a favorable way for *P. lambertii*. The most relevant differences were found when the sun is at its highest position in the sky (Fig. 2). Accordingly, from 1100 to 1300 hours, the recorded temperature was 15 % lower inside the corridors and 11 % lower in the adjacencies, while air relative humidity was 32 % and 21 % higher in the corridors and adjacencies when compared to the atmospheric values, respectively. These differences found are all statistically significant (Table 1). On the other hand, no differences were found between the surrounding vegetation microclimate and the atmosphere.

Similar results were found with the linear regression analyses. All linear regressions are statistically significant with high values of determination index (R^2) (Fig. 3). However, the linear regression slope values differ among these three microenvironments, with a consistent decreasing tendency from the

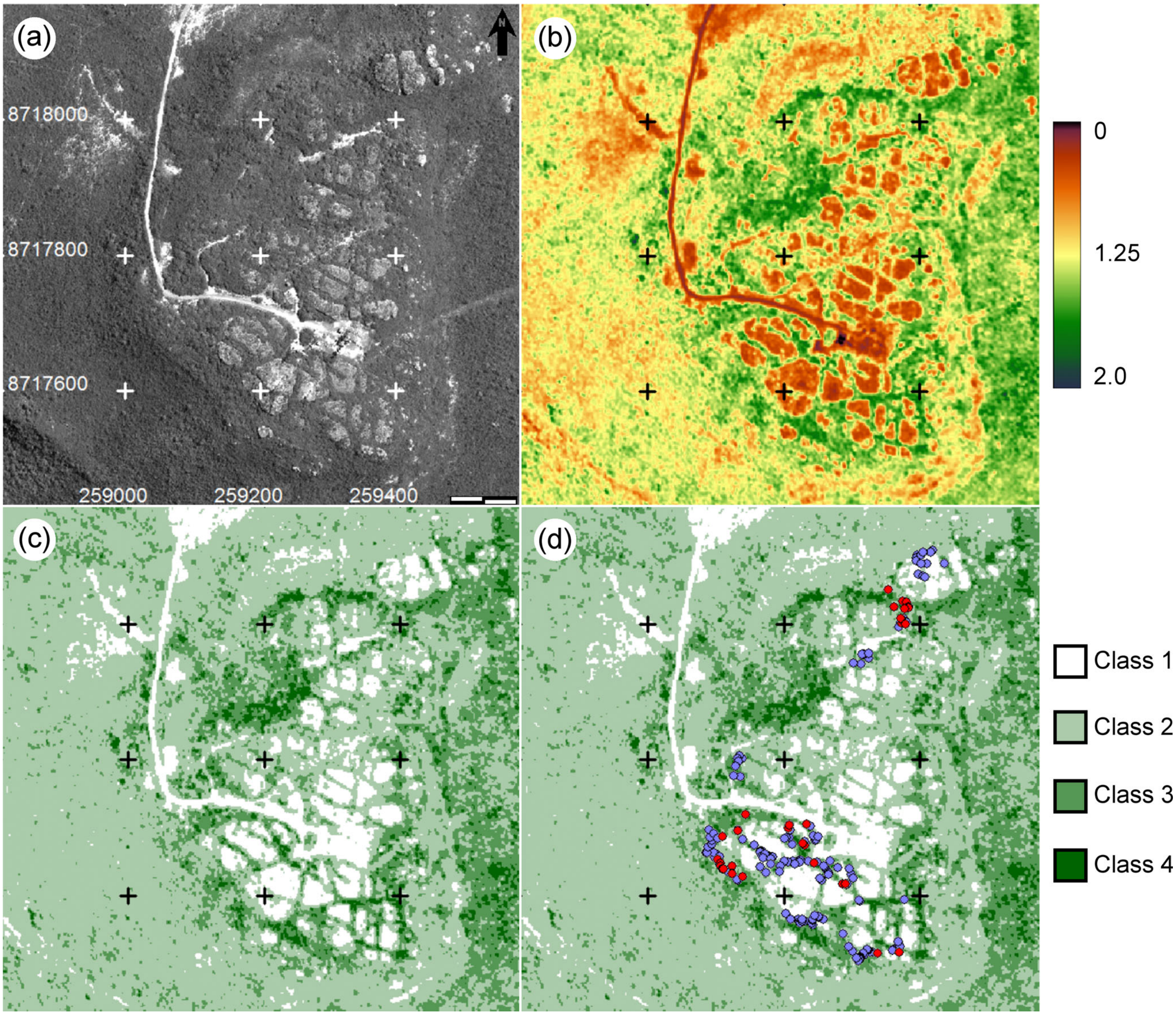

Fig. 3 Results of the remote sensing analysis of the sampling site. **a** Sampling site panchromatic image showing the rock outcrops (resolution 0.5 m and scale bar=100 m). **b** Leaf area index (LAI) image. Lower values of LAI are indicated in red, and higher values of LAI are indicated in green (resolution=2 m). **c** Reclassified image using the following range of LAI values: class 1 shows areas with rock or naked soil. Class 2 shows areas with low LAI vegetation. Class 3 shows areas with medium LAI vegetation. Class 4 shows areas with high LAI vegetation. **d** Reclassified image with all sampled individuals, both alive (*blue*) and damaged or dead (*red*)

Table 1 Comparison of temperature and relative humidity among sites

	Temperature (°C)			Relative humidity (%)		
Kruskal-Wallis	X^2=60.7 Mean	df=3 STD	p<0.0001 Groups	X^2=51.3 Mean	df=3 STD	p<0.0001 Groups
Atmosphere	32.4	0.8	A	37.1	3.0	A
Vegetation matrix	31.7	0.9	A	39.3	2.7	A
Adjacencies	29.3	0.5	B	45.0	3.4	B
Corridors	27.5	0.3	B	49.0	3.0	B

Values of these two microclimatic variables represent the period between 1100 and 1300 hours. The results of nonparametric multiple-comparison analysis are also shown. Different group letters indicate differences between sites

surrounding vegetation matrix toward the corridors. Both slope values for temperature and relative humidity in the surrounding vegetation are close to 1.0. Nonetheless, the slope values for temperature are 22 and 42 % smaller in the adjacencies and corridors when compared to the surrounding vegetation, respectively. Differences are slightly smaller for relative humidity, and they are 11 and 20 % smaller in the adjacencies and corridors, respectively. All these differences are statistically significant according to the ANCOVA and its post hoc analyses (Table 2).

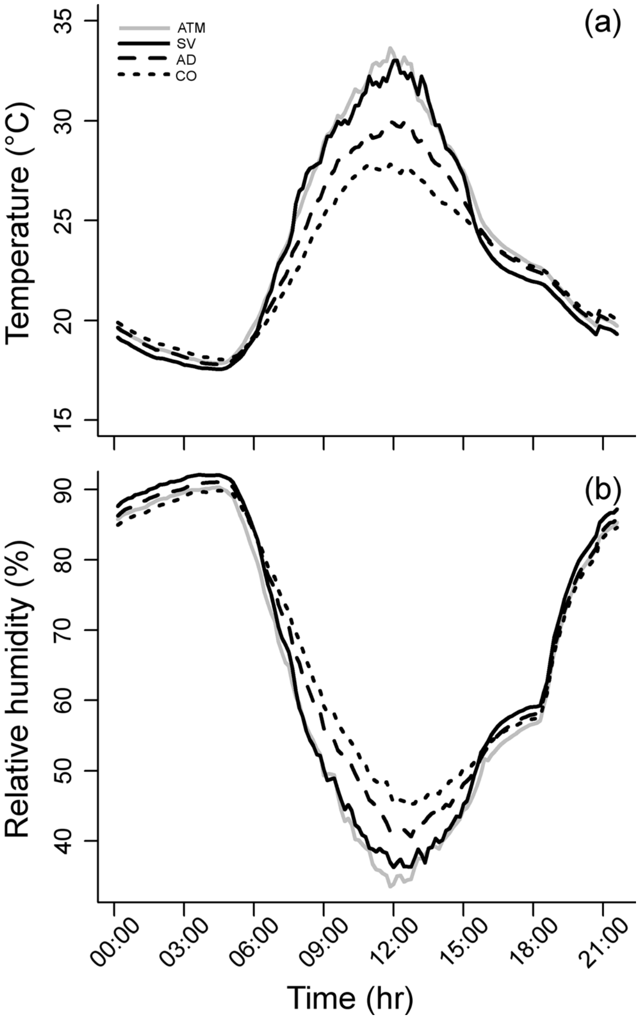

Fig. 4 Daily variation of **a** temperature and **b** air relative humidity in the three environmental categories: surrounding vegetation (SV), adjacencies (AD), and corridors (CO), and the atmosphere (ATM)

Vegetation characteristics

Differences are also evident in the vegetation characteristics as imaged by satellite (Fig. 4). The vegetation on hilltops, in areas protected by the outcrops, showed higher values of LAI. This means that this vegetation has higher values of leaf area per ground area, in contrast to the surrounding vegetation that is mainly formed by shrubs and small trees. Classes shown in Fig. 4c were built using different ranges of LAI values. Individuals of *P. lambertii* are mainly found in class 4 areas. Apparently, clusters of damaged and dead individuals are located in the least protected areas (Fig. 4d). It is important to highlight that some shorter rock outcrops with a dense vegetation cover on top were not distinguishable in the LAI images and its classes, resulting in some distortions that could limit this method.

Population structure

The results of the population structure analysis (Fig. 5) show that few individuals reach heights of more than 6 m and diameters wider than 15 cm. However, we found a high number of saplings in the field. It is important to highlight that the height of *P. lambertii* trees is strongly limited by the height of the closest rock outcrop. The determination index (R^2) for the relationship between tree and rock outcrop height is 0.82. On the other hand, the diameter of the same individuals is not strongly related to the rock outcrop height (R^2=0.11).

Tree growth

Studied individuals showed frequent wedding rings that could merge up to five rings into one. Although wedding rings were relatively common, we were able to date 31 from 42 sampled specimens. The maximum length of the chronology is 138 years, though the EPS indicates that the chronology is well replicated until 1920 (Fig. 6). This means that the

Table 2 ANCOVA and post hoc analyses results for temperature and relative humidity

ANCOVA	Temperature					Relative humidity				
	df	S squares	M squares	*F*	*p*	*df*	S squares	M squares	*F*	*p*
Atm	1	50301	50301	138460	<0.0001	1	961137	961137	205179	<0.0001
Microenv	2	518	259	713	<0.0001	2	1451	726	155	<0.0001
Atm×microenv	2	1939	970	2669	<0.0001	2	7989	3994	853	<0.0001
Resíduos	1902	691	0			1902		5		
Post hoc										
		Estimate	Std. Error	t	p		Estimate	Std. Error	t	p
SV-CO		0.5485	0.0338	−21.43	<0.0001		1.2894	0.1214	10.624	<0.0001
SV-AD		−0.7242	0.0338	16.23	<0.0001		−0.8305	0.1214	−6.843	<0.0001
AD-CO		1.2728	0.0338	37.66	<0.0001		−2.1199	0.1214	−17.466	<0.0001

Significant *p* values for the interaction between the atmosphere and the microenvironmental categories (Atm×Microenv) indicate that the regression slope differences are statistically significant. Differences between pairs of the three microenviromental categories were tested using a post hoc test

SV surrounding vegetation, *AD* rock outcrops adjacencies, *CO* rock outcrops corridors

chronology is robust within this period and that it could be used in the climate/growth analysis. Furthermore, the chronology has an inter-series correlation of 0.44 and a mean sensitivity of 0.67. Tree ring width is relatively small with an average value of 0.92 mm (Table 3).

Climate/growth correlations (Fig. 7) show that climate during the beginning of the current growth season and the middle of the previous growth season played an important role in the growth of this species. Precipitation, days of precipitation, and cloud cover in November have a positive effect on tree-ring

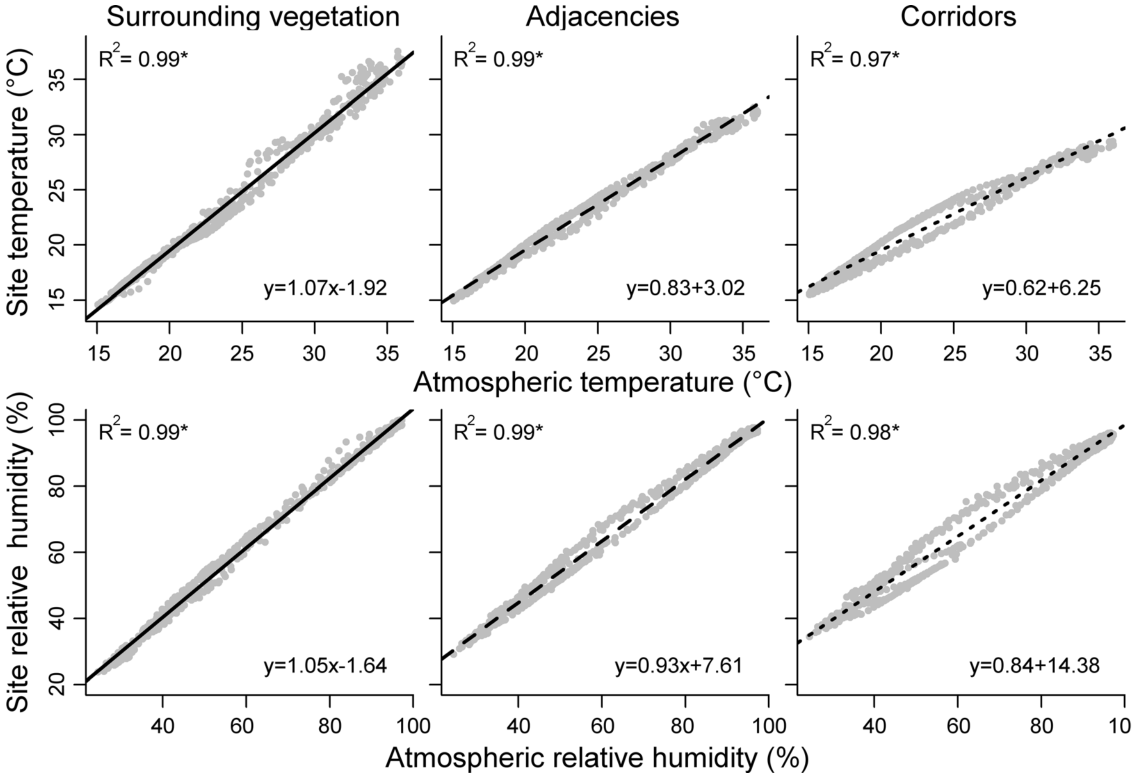

Fig. 5 Linear regressions of relative humidity and temperature between each microenvironment and the atmospheric data. The determination index and the linear equation are provided for each regression. Asterisk indicates statistically significant for p value smaller than 0.05

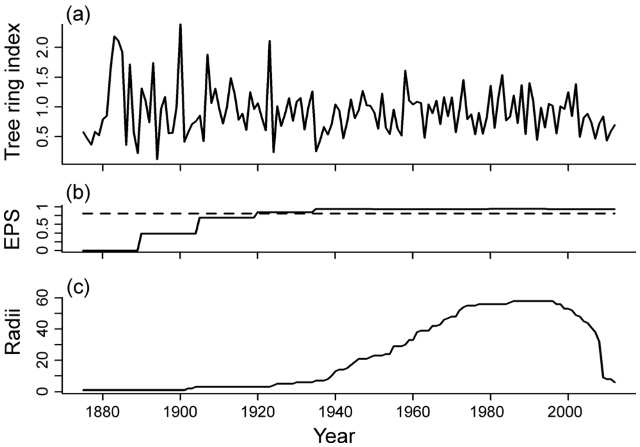

Fig. 6 **a** Residual chronology based on 31 specimens of *P. lambertii*. **b** Calculated EPS for the dated tree rings. *Dashed line* indicates the EPS value of 0.85. **c** Sample depth graphic showing the length in years of all dated radii

width, while maximum temperature of November and December and hours of sun in September have a negative effect on radial growth. For the previous growth season, days of precipitation in January have a positive effect on radial growth, whereas maximum temperature in December and January has a negative effect on it. Overall, the correlations with current season climate variables are slightly higher than those from the previous season.

Out of the three tested models, the one with temperature and precipitation was the best model as tested by AIC (Table 4). This model shows that both variables have distinct effects on wood formation (Table 5). Temperature has a higher value of explained percentage (35.3 %) than precipitation (18.2 %). The small difference in the number of observations among the correlation analyses and the linear model is a result of the gaps found in the time series of each variable.

Discussion

Methodological constraints

Past research showed less than ideal wood features in *Podocarpus* spp. for dendrochronological studies, for instance, poorly defined tree-ring boundaries (Bauch et al. 2006; Buckley et al. 1995), high amount of wedding rings, and the presence of lobate stem growth (Dunwiddie 1979; Buckley et al. 1995; Krepkowski et al. 2012; February and Stock 1998; Ferrero et al. 2014). Despite these typical problems, McDougall et al. (2012) successfully dated individuals of *Podocarpus lawrencei* in the Australian Alps. In this population, authors also described the negative impact of wedding rings and lobate growth on dating. In that study, they were able to date 52 % of sampled trees. We also found wedding rings, but no lobate growth, in *P. lambertii*, that resulted in 73 % of dated trees. As highlighted by McDougall et al. (2012), stem discs were also essential for the precise dating of *P. lambertii* tree rings. An additional common feature between both studies is that the populations were from areas with clear limiting conditions, either relatively high altitude or low latitude.

Table 3 Chronology diagnostic showing the number of dated trees, maximum and mean series length (years), inter-correlation among series (IC), mean sensitivity (MS), and mean and standard deviation of tree-ring width

Trees	Max length	Mean length	IC	MS	Mean TRW	STD TRW
31	138	54.3	0.44	0.67	0.92	0.74

Mean TRW and STD TRW, respectively, units in millimeters

Rock outcrop effect in *P. lambertii*'s growth

At 11° of southern latitude, the individuals of *P. lambertii* analyzed in the current study belong to the northernmost limit of the present-day distribution for this species. There, the presence of the rock outcrops seems to decouple regional climate in a favorable way for *P. lambertii*. On one hand, the microclimatic in the surrounding vegetation, where this species is not found, is similar to the atmospheric conditions. On the other hand, the rock outcrops can reduce the atmospheric temperature up to 4.9 °C and increase the air relative humidity up to 12 %. Not only it changes the average values but it also reduces the variability of temperature and air relative humidity, with a stronger effect on the former one. From all elements of topography that potentially influence the microclimatic conditions, concave formations seem to have a stronger capacity of climate decoupling (Dobrowski 2011; Hylander et al. 2015), like the corridors and adjacencies found in the study site.

Actually, the presence of rock coutcrops allows a different vegetation structure to inhabit the semiarid. Leaf area index from the protected areas is closer to the values found in mixed forests and deciduous broadleaf forests. Meanwhile, the LAI values from the surrounding vegetation matrix are similar to the LAI from woody savanna areas (Zhu et al. 2013). Rock outcrops can host species that have a disjunctive distribution and are far from their macroclimate optimum (Speziale and Ezcurra 2012). Similar to the *P. lambertii* site in northeast Brazil, species found in areas protected by rock outcrops are different from those inhabiting the surrounding vegetation matrix. They are also components of colder vegetative areas in the south.

The importance of the rock outcrops to *P. lambertii* is evident, not only because specimens grow in their adjacencies and corridors but also because the maximum tree heights are constrained by the rock outcrop height. Apparently, the favorable microclimate is restricted up to the rock outcrop edge, above which the mesoclimate prevails. However, to understand the real positive impact of the microclimate provided by this rock formation, we must know what limits the

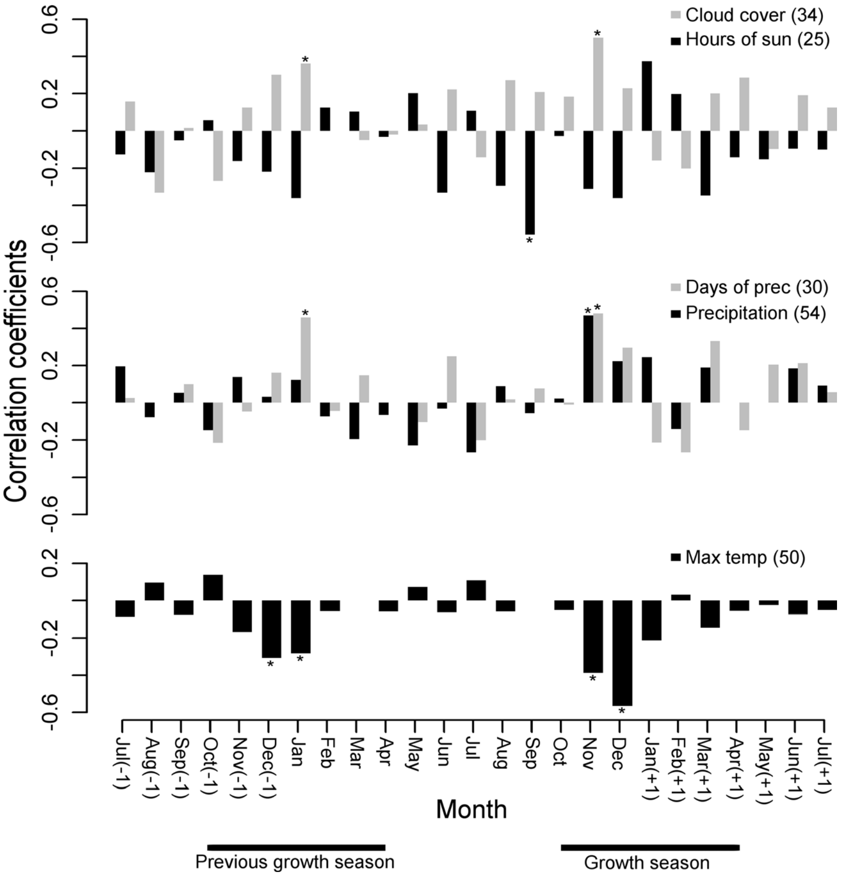

Fig. 7 Monthly correlation among residual chronology and the following climate variables: hours of sun, cloud cover, days of precipitation, precipitation, and maximum temperature. Correlations were calculated for the current and previous growth seasons. Negative labels for the months designate the previous calendar year, and positive values designate the next calendar year. Values shown in parentheses are the length of the available time series. *Asterisk* indicates statistically significant for p value smaller than 0.05

development of *P. lambertii* at that site. The climate/growth correlations and models showed that maximum temperatures during the beginning of the current and past growth seasons have a negative impact on the growth of this species. These results indicate that (1) this species is strongly limited by high values of maximum temperature and (2) temperatures during midday regulate the growth of *P. lambertii*. That is precisely when temperature differences between areas protected by rock outcrops and unprotected areas are maximized.

It is important to highlight the climatic hierarchy between the climate data used in the growth models—mesoclimate—and the actual microclimatic conditions that affect these trees' growth. The mesoclimate modulates the local climate, which in turn modulates the microclimate (Geiger et al. 2009) in the areas inhabited by *P. lambertii*. Although a decoupling exists, high mesoclimatic temperatures will result in proportional higher temperatures in the areas protected by the rock outcrops, as well as lower mesoclimatic temperatures will result in proportional lower temperatures in the same sites. Nonetheless, the range between higher and lower temperatures will be always narrower in the protected areas, as our results showed. Moreover, this relation between the temperature of protected and nonprotected areas by elements of topography seems to be consistently linear (e.g., Ruzicka et al. 2015).

Other conifer species, like *Pinus sylvestris* and *P. nigra* in the Mediterranean basin, *Tsuga canadensis* in North America, and *Abies alba* in the Italian Alps, showed similar constraint at their low latitude distribution limit, also known as rear edge

Table 4 Linear models comparison for climate/growth relationships in *P. lambertii*

Linear model	AIC
Res=MaxTemp (Dec)+Prec (Nov)	−27.3
Res=MaxTemp (Dec)	−13.1
Res=Prec (Nov)	−7.6

The smallest AIC indicates the best model (for differences higher than 2)

Table 5 Description of the best climate/growth model for *P. lambertii*, as indicated by the AIC

N=49, R^2=53.5 Variables	R^2_{adj}=51.5 Coefficient	P<0.0001 Exp. percentage (%)
Intercept	3.503	–
MaxTemp (Dec)	-1.049×10^{-1}	35.3
Prec (Nov)	1.642×10^{-3}	18.2
Residuals	–	46.4

The number of observations (N), determination index (R^2), adjusted determination index for the number of variables (R^2_{adj}), p values, coefficients, and explained percentage is given populations (Herrero et al. 2013; Hart et al. 2010; Carrer et al. 2010). All of them had a comparable history of expansion during a colder and wetter period and contraction during warmer and drier periods. Those populations seem to be systematically constrained by drought stress. Although precipitation also seems to be relevant, their distribution is mainly limited by temperature-induced stress. This pattern is not only limited to conifers, but it is also reported for eudicots like Fagus spp. (Fang and Lechowicz 2008; Tegel et al. 2014).

Although the influence of precipitation on *P. lambertii* tree ring width is almost half of temperature influence, it is certainly a relevant variable for the growth of this species. Unfortunately, we cannot statistically separate the effects of precipitation, days of precipitation, and cloud cover because they have different time series lengths. This fact does not allow testing collinearity among them using linear models. Nevertheless, they may be acting concurrently, and high amounts of well-distributed precipitation during the beginning of the growth season could be important for the growth of this species in well-drained sand soil. Regarding the cloud cover variable, it is usually related to the reduction of evapotranspiration, as well as drought stress (Fischer et al. 2009).

Even though rock outcrop corridors produce a more favorable microclimate for the growth of *P. lambertii*, we cannot say that it fully emulates the climate conditions from its main distribution area. First, individuals from this population must exert wood and leaf anatomical plasticity to survive in those conditions (Locosselli and Ceccantini 2012). Second, the average radial growth of these specimens is 0.9 mm, which is three times smaller than the growth reported for a population some 1980 km to the south with an average value of 2.7 mm (Mattos et al. 2007). In another site at 1750 km to the South of Morro do Chapéu, Canetti et al. (2014) report a radial increment of 4 mm per year in the same species. In fact, specific trait differences are expected between populations inhabiting microrefuge and the distribution core (Mee and Moore 2013). Despite these trait differences, we actually found no strong evidence of population decline. Surprisingly, several seedlings were found during fieldwork, as represented by population structure results. This probably means that these adaptations and the climate shelter by outcrops have thus far been effective.

It is well known that species ranges are highly dynamic and that they expand and contract according to changes in environmental conditions (Sexton et al. 2009). Usually, small populations at the distribution limit, such as this *P. lambertii* population, are more vulnerable to environmental changes (Willi et al. 2006; Mee and Moore 2013). Therefore, the studied population could be in a threatened position in the context of fast climate changes from global warming (IPCC 2007), especially if the predicted changes are beyond the ability of this species to mount sufficient phenotypic plasticity to adapt and/or beyond the capacity of rock outcrops to decouple local climate in a way that favors *P. lambertii*.

Conclusion

Rock outcrops decouple the mesoclimate by reducing temperature and increasing relative humidity in the protected areas. Out of these two variables, the decoupling effect of the rock outcrops seems to be stronger on the temperature. This favorable condition allows a vegetation with higher LAI to inhabit these protected areas where the individuals of *P. lambertii* are found. Additionally, specimens height is constrained by the outcrops height suggesting that the favorable microclimate is restricted up to the rock outcrop edge. Tree-ring analyses showed that temperature is the limiting growth factor for this population, which in turn is the measured microclimatic variable that is mostly affected by the rock outcrops. Therefore, these topographic elements can be regarded as essential for the growth and survival of this population.

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