

ABUNDANCE AND VIGOR OF THREE SELECTED UNDERSTORY SPECIES ALONG ENVIRONMENTAL GRADIENTS IN SOUTH-EASTERN BRAZIL

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Abstract. The majority of floristic and phytosociological studies conducted in the Atlantic Forest are focused on tree species and tree species communities, while only limited research is done on understory species, in particular concerning their interrelationship with environmental factors or their ecological requirements in terms of habitat change due to anthropogenic influences, such as complete and selective logging. In our study, the species abundance and vigor of three representative species of the Atlantic Forest in south-eastern Brazil (Gesneriaceae: *Nematanthus crassifolius*, *Besleria melancholica*; Acanthaceae: *Stenostephanus lobeliaeformis*) were measured in a riverine ecosystem that included different levels of past logging activities along environmental gradients such as altitude, exposure, inclination, and canopy openness. We measured the vigor of the species by counting the total number of shoots and estimating the rate of live shoots. To provide a comprehensive overview we developed a vigor index based on this data which might be useful for future studies on the response to environmental gradients of understory species in the tropics. The results show distinct relationships between various environmental factors and both species distribution patterns and vigor of the investigated species. *N. crassifolius* is strongly dependant on proximity to watercourses and open canopy conditions. Abundance of *S. lobeliaeformis* was limited to higher elevations, but according to our data individuals of this species are more vigorous at lower elevations of its distributional range. While being more vigorous with decreasing elevation, *S. lobeliaeformis* was completely absent at the lower end of the elevation gradient. The abrupt absence of this species at low elevations coincides with a complete forest clearance in the 1940s. *S. lobeliaeformis* was only found in the selectively logged forest. In contrast, changes in abiotic conditions have little effect on *B. melancholica*. We conclude that small-scale elevational and microclimatic gradients have differing consequences for the selected understory species. Those natural gradients are disturbed by a land-use gradient, and a scenario like this is typical of the Atlantic Rainforest at this elevation. Therefore a further understanding, especially of the largely undersampled understory plant community, is essential and a first approach in this direction is provided by this study.

Key words: *Acanthaceae*, Atlantic Rainforest, distribution pattern, disturbance history, *Gesneriaceae*, vigor.

INTRODUCTION

The Atlantic Rainforest (“Mata Atlântica”) is a highly diverse ecosystem with an outstanding level of endemism (Fonseca 1985, Prance 1987, Morawetz & Krügel 1997), but is currently threatened by ongoing habitat loss and increasing forest fragmentation (Ranta *et al.* 1998, da Silva & Tabarelli 2000, Oliveira-Filho & Fontes 2000, Tabarelli *et al.* 2005, Ribeiro *et al.* 2009). The remaining remnants are a mosaic of small, abiotically and biotically heterogeneous areas (Lima & Capobianco 1997, Gascon *et al.* 1999). Comprehensive knowledge of their struc-

tural and floristic diversity is required for developing conservation strategies (de Barcellos-Falkenberg & Voltolini 1995, Metzger 1997, Morellato & Haddad 2000).

There is little information about the structure and floristic composition of plant communities in Neotropical montane forests (Madsen & Øllgaard 1994), particularly as regards changes in species composition along altitudinal gradients within the same geographic level (Cavelier 1996, Aiba & Kitayama 1999, Kessler 2001). Only a few studies on the influence of small-scale altitudinal changes on communities of trees, lianas, and herbaceous plants have been carried out to date (Liebermann *et al.* 1985,

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Horvitz & Le Corff 1993, Freiberg & Gottsberger 2001).

The local climate plus environmental and/or historical factors are the main elements determining species composition in tropical rainforests on a regional scale (Webb 1968, Whitmore 1973, Hall & Swaine 1976), but there exists a hierarchy of different influences within a given climatic region. The fragmented Atlantic Rainforest is a mosaic of different disturbance scenarios, showing a complex history of logging events of varying degrees. The interdependence between such anthropogenic impacts and the requirements of the vegetation is of great interest when attempting to understand the ecological consequences at the species level.

Most of the published results of floristic and phytosociologic studies in south-eastern Brazil focus on woody plants forming the canopy layer (Andreatta *et al.* 1997). Nevertheless, herbaceous plants of the understory contribute significantly to species richness in tropical plant communities, representing 20–50% of the local diversity of vascular plants (Gentry & Dodson 1987, Gentry & Emmons 1987, Andreatta *et al.* 1997, Duque *et al.* 2002). However, there is a lack of knowledge about limiting factors and the key influences of environmental gradients on the abundance, vigor, and growth of understory species (Liebermann *et al.* 1985, Freiberg 1994, Freiberg & Gottsberger 2001, Drucker *et al.* 2008).

We examined the relationship between potentially key environmental factors, such as elevation, inclination, exposure, distance to river, and canopy openness, and individual species performance. Each of those parameters is a describing variable for microclimatic conditions affecting the understory plant community. Lopes *et al.* (2005) identified numerous microhabitats in the Atlantic Rainforest that are essential to the diversity of understory species, given the heterogeneity of local topography and environmental conditions. Our study continues this work and extends our knowledge of the response of species to environmental gradients.

Besides gaining knowledge of the ecology of understory plants it is important to evaluate the influence of differing disturbance history, in terms of logging, in varying dimensions. It remains uncertain to which degree each of those components relates to the understory community.

We developed a vigor-index, based on growth variables, to quantify the health conditions of the

studied species. Additionally, this index might be a useful tool to standardize the results and to enhance the comparability of further studies.

The three studied species (Acanthaceae: *Stenostaphanus lobeliaeformis* Nees; Gesneriaceae: *Besleria melancholica* (Vell.) C.V. Morton, *Nematanthus crassifolius* (Schott) Wiehler) are typical understory herbaceous plants of the coastal rainforest in the state of Rio de Janeiro. The differences in their distribution are presumably a result of habitat and microclimatic heterogeneity. Thus we predict different requirements as regards environmental conditions for each species.

The main questions to be answered in our study are:

- (1) Which environmental factors are related to the abundance and vigor of the three species?
- (2) How does the interdependency between environmental gradients and the studied species change in a forest with different historical and recent logging impacts?

METHODS

Study area. The study was conducted from April to September 2007 in the Atlantic Rainforest (“Mata Atlântica”) of the state of Rio de Janeiro, Brazil in the private reserve “Reserva Ecológica de Guapiaçu” (REGUA – 22°25'53”S, 42°45'20”W) in the municipality of Cachoeiras de Macacu. The 5500-ha reserve is located on the south-facing slopes of the Serra dos Órgãos Mountain range, about 100 km from the city of Rio de Janeiro, and covers an altitudinal gradient from 30 to 2200 m a.s.l. Most of the mid- to high-elevation forests are protected at State Park level. The mean annual temperature for this region is about 23°C with a mean annual rainfall of about 2560 mm. There is a hot and rainy season from October to March and a cooler and drier season from April to September (Kurtz & de Araújo 2000).

The vegetation can be classified as an evergreen dense ombrophilous forest (Veloso *et al.* 1991) that is typical for the lower and medium elevations of the coastal mountain range (Morellato & Haddad 2000, Oliveira-Filho & Fontes 2000). Due to forest logging for agriculture on the property of REGUA since the beginning of the 20th century (Locke, pers. comm.) there are now vegetation formations of several succession stages. The oldest parts of the regrown forest are mostly connected to the continuous forest of the mountain range and are now turning into mature

forest. In the lower parts of REGUA, and within the areas used as pasture and agricultural land, the forest is highly fragmented and disturbed.

Study species. We selected three understory species which are common in the study area and easy to recognize (Acanthaceae: *Stenostephanus lobeliaeformis* Nees, Gesneriaceae: *Besleria melancholica* (Vell.) C.V. Morton; *Nematanthus crassifolius* (Schott) Wiehler).

Species of the family Acanthaceae grow in diverse habitats like forests, swamps, or pastures. Because of the species richness within this family (app. 85 genera and 2000 known species in the Neotropics) there is a huge lack of knowledge about the distribution, endemism, and ecological requirements of individual species (Wasshausen 2005).

Stenostephanus lobeliaeformis Nees (Acanthaceae):

This species is an erect perennial woody herb and grows as a ramified sub-shrub with a height of up to 1.50 m. The genus contains about 39 species which are common within cloud forests, along riversides and in wet dips (Daniel 1999). Its distribution is exclusively neotropical and ranges from southern North America to Colombia and Brazil. *S. lobeliaeformis* is listed as a vulnerable species in the state of Espírito Santo in Brazil.

The family of Gesneriaceae is a useful indicator group in vegetation classification studies in the tropics according to criteria like specialization of individual species to habitat and easy recognition in the field (Kessler & Bach 1999). Many species are endemic to geographically small areas or, the majority, restricted to specific habitats (Denham 2004) and generally disappear when habitats face sustained disturbance. They can be regarded as indicators for the diversity of flowering plants and as representatives of the status of the whole flora of a given area (Skog 2005).

The life forms of the common genera *Besleria* and *Nematanthus* are species-specific as well as habitat-dependent. They appear as herbs, sub-shrubs or shrubs and grow terrestrially, hemiepiphytically, or epiphytically. Those life forms show different requirements regarding abiotic factors like light intensity, humidity, and soil characteristics (Lopes *et al.* 2005).

Besleria melancholica (Vell.) C.V. Morton (Gesneriaceae):

The genus *Besleria* is one of only a few genera of Gesneriaceae whose species grow as shrubs or even small trees. *Besleria melancholica* is a perennial shrub endemic to the coastal Atlantic rainforest of the state

of Rio de Janeiro. It grows around the city of Rio de Janeiro and in the Serra dos Órgãos at elevations of between 150 and 1200 m a.s.l. The genus is common in the understory of pluvial forests in shady habitats near slopes and waysides (Lopes *et al.* 2005, Kriebel-Haehner 2006).

In the Neotropics the genus is one of the most diverse genera within the Gesneriaceae, comprising about 160 species, at least 16 of them occurring in Brazil (Chautems 1991 and pers. comm.).

Nematanthus crassifolius (Schott) Wiehler (Gesneriaceae):

N. crassifolius is an obligate epiphytic or accidentally epilithic species (Chautems 1988). The climbing or pendulous shoots are slightly lignified and hairless. This species is endemic to the Atlantic rainforest of south-eastern Brazil (Lopes *et al.* 2005) and has been recorded in the states of Espírito Santo, Minas Gerais, Rio de Janeiro, and São Paulo growing at elevations of between 50 and 1500 a.s.l. (Chautems and Kiyama 2003, Chautems, pers. comm.). The pubescent and oval-elliptical leaves are anisophyllous with green glossy upper surface, whereas the underside is infrequently red-magenta in color. This variance is interpreted as an ecotype (Blanc 2002).

N. crassifolius is frequently found near riversides and occurs sometimes as isolated individuals in the forest interior (Lopes *et al.* 2005).

Study design. Starting about 100 m downriver of a waterfall we established six transects along the Rio Manuel Alexandre. Each transect was 100 m in length and 10 m wide, separated into two 50-m subtransects on each side of the river at right angles to its course (Hoagland & Collins 1997). Each subtransect was divided into five plots of 10 m x 10 m each (Annaselvam & Parthasarathy 2001, Freiberg & Gottsberger 2001), resulting in a total of 0.1 ha for every transect. They were located within a minimum distance of 250 m (along the course of the river) of each other. During the establishment of these transects, tributaries were avoided and the accessibility of the waterside was taken into consideration to prevent a disarrangement of the transect line (Fernández-Aláez *et al.* 2005). The three upper transects (400-320 m a.s.l.) were situated in a forest formation where selective logging took place until the 1970s, whereas the other three transects at a lower elevation (250-200 m a.s.l.) were located within forest which was completely felled around the 1940s (Locke, pers. comm.) (Fig. 1).

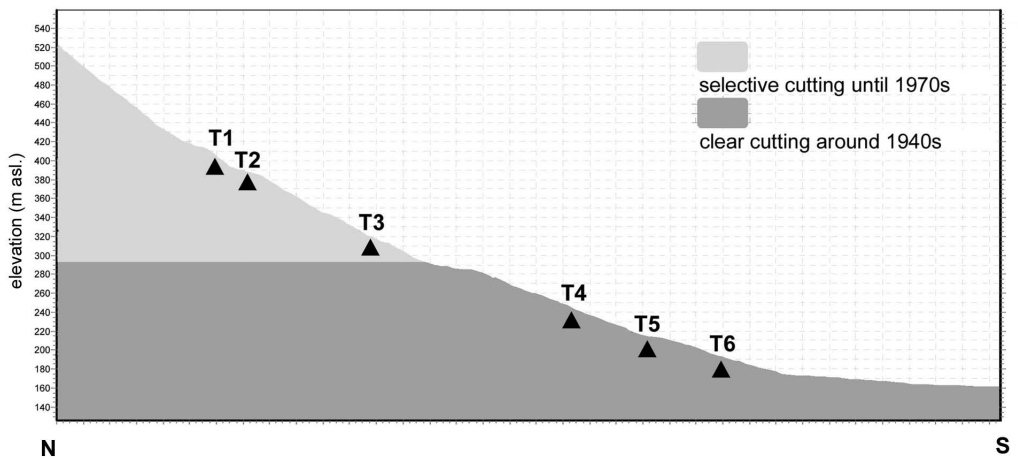
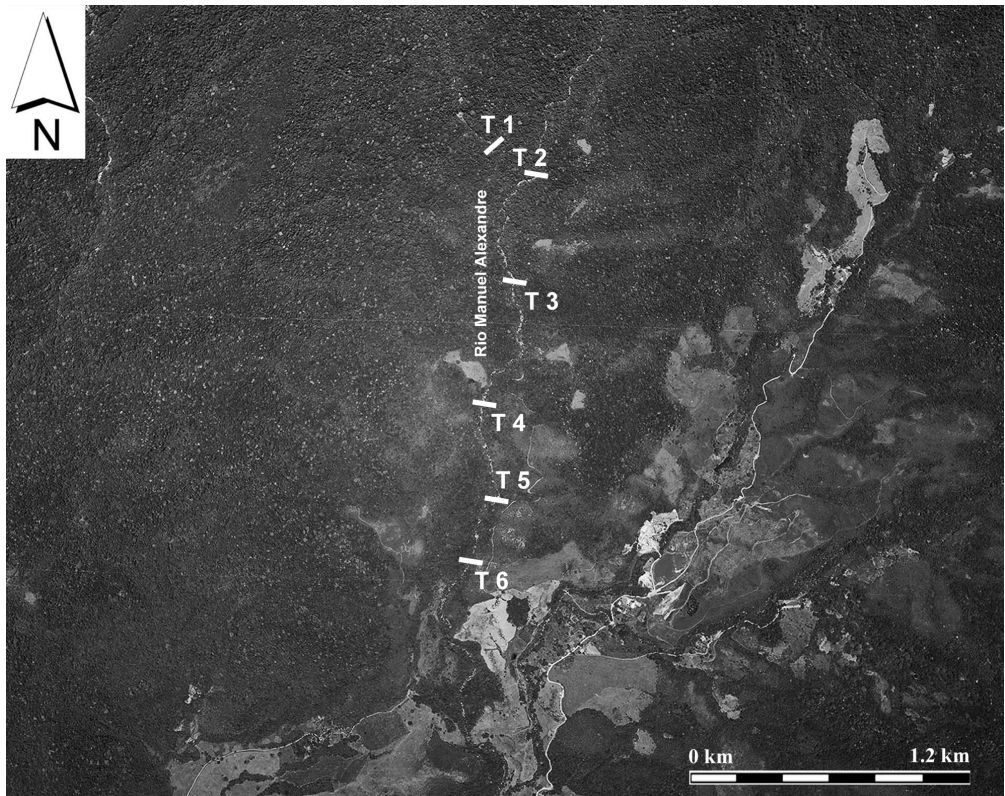


FIG. 1. Location of the research transects along the Rio Manuel Alexandre within the area of the “Reserva Ecológica de Guapiaçu” (REGUA – 22°25’53”S, 42°45’20”W) including the elevation profile of the river course and the logging activities in the forest. (Aerial photograph source: Mr. Nicholas Locke, REGUA).

In every plot the following abiotic parameters were measured: altitude, distance to river, inclination and exposition, as well as canopy openness. Altitude was measured with a barometric altimeter (Suunto™ Vector) and distance to the river was determined by measuring tape. To obtain inclination data we made an inclinometer out of a simple 180° protractor by fixing a plumb line at 90°, which referred to zero degree inclination. By holding the inclinometer parallel to the slope we measured the inclination. Exposition was measured with a standard compass. To use exposition as an analyzable environmental factor it was transformed into a non-circular variable by calculating the sinus of the exposure degrees, whereby exposure is denoted as “easterness”. Canopy openness was measured by taking hemispherical photographs at the center of each 10 x 10-m plot. We used a Nikon Coolpix 4500 digital camera in combination with a Nikon FC-E8 fisheye-lens. Resolution was set to 2272 x 1704 pixels. The camera was fixed on a tripod 1.30 m above the ground, leveled and looking upwards to the sky. Pictures were only taken under overcast conditions to avoid overexposure and to reduce reflections on leaves which could be construed as openings (Trichon *et al.* 1998, Williams *et al.* 2003). The WinScanopy 2005ab software (Regent Instruments Inc. 2005) was used to analyze the hemispherical photographs and to derive canopy openness data. Canopy openness is defined as the proportion of open sky area in a 180° hemisphere monitored from a central point. Pixels of digital images are to be classified as either “canopy” or “sky” based on the grayscale value (pictures are automatically transformed to grayscale from color photographs by the software).

Abundance and vigor of all individuals of the investigated species were recorded. All individuals of all three species were counted in every plot per transect. The total number of shoots, and the number of living ones, was acquired per plant individual. Living shoots were estimated in length and classified into two size classes (small 0-60 cm, large > 60 cm). This method was chosen because most individuals of *N. crassifolius* were growing as epiphytes and therefore were situated out of reach for exact measurements. Using shoots as a morphological trait for vigor estimation in tropical understory plants is an established method (Bruna *et al.* 2002)

The following characteristics were selected as indicators of vigor and combined into a vigor-index for every individual:

$$V = \frac{ShL_{Ind}}{ShT_{Ind}} \left(\frac{ShB_{Ind} + 1}{2} \right) \left(\frac{ShT_{Ind}}{ShM_{Pop}} \right)$$

- ShL_{Ind} number of living shoots on individual plant
- ShT_{Ind} total number of shoots on individual plant
- ShB_{Ind} number of living shoots in large size class
- ShM_{Pop} maximum number of living shoots per individual in the investigated population
- V vigor-index score

The index ranges from 0 to 1 with the higher-scoring individuals being more vigorous. The peak value of 1 is reached for an individual with the maximum number of shoots in the whole investigated population, all of them alive and in the large size class, whereas a value of 0 indicates an individual without any living shoots.

Statistical analysis. Because of the division of 100-m transects into 10 plots of 10 x 10 m each, the individual plots are located side by side. Thus the statistical treatment of those areas as independent units might be questionable in terms of the effect of spatial autocorrelation (e.g. Legendre 1993, Diniz-Filho *et al.* 2008). There are two commonly used indices to test for spatial autocorrelation. Moran's *I* (Moran 1950) is a measure of global spatial autocorrelation, while Geary's *C* (Geary 1954) is more sensitive to local spatial autocorrelation and was used in this case. Geary's *C* was calculated using ROOKCASE (Sawada 1999).

$$C = \frac{(N-1) \sum_i \sum_j \omega_{ij} (X_i - X_j)^2}{2W \sum_i (X_i - \bar{X})^2}$$

- N number of observations
- i, j location within transect (plot)
- X variable of interest (abundance of species, canopy openness, inclination)
- ω_{ij} distance (spatial lag) between locations i and j
- W sum of all ω_{ij}

The value of Geary's *C* lies between 0 and 2. Geary's *C* approaches 1 when the spatial pattern is close to random, and it is less than or greater than 1 when the spatial pattern is respectively clustered or dispersed.

We tested for spatial autocorrelation in distribution of the studied species and environmental variables (canopy openness and inclination). Para-

TABLE 1. Geary's C (local spatial autocorrelation) for species distribution and data apportionment of non-spatial environmental factors in all transects.

Geary's C	T1	T2	T3	T4	T5	T6	mean
<i>Stenostephanus lobeliaeformis</i>	0.91	1.21	0.97	1.11	-	-	1.05
<i>Besleria melancholica</i>	1.12	0.68	1.12	-	-	-	0.97
<i>Nematanthus crassifolius</i>	-	0.98	0.5	0.77	0.57	1.11	0.79
canopy openness	0.96	0.9	0.6	1.48	0.76	0.19	0.81 (0.94) ¹
inclination	0.39	0.71	0.81	0.79	0.85	0.16	0.62 (0.71) ¹

¹ value in parentheses excluding T6

meters with a direct spatial reference (distance to river and exposition) were excluded from the analysis. In the majority of cases the results show a distribution close to a random spatial pattern (Table 1), with the exception of environmental variables in T6 because of the almost complete clearing of the steep eastern part of this particular transect.

The outcome of the spatial autocorrelation analysis of our data indicates a general random spatial pattern of the variables at the given scale and therefore plots can be statistically treated as independent units.

To check on redundant information within the environmental variables we additionally used the nonparametric Spearman Rank Order Correlation. Only a single significant correlation was detected between canopy openness and elevation. Although the relation between both factors is not exceptionally strong ($r = -0.437$, $P < 0.001$) it has to be kept in mind when interpreting further results.

To examine if the species distribution was related to the environmental variables we performed a redundancy analysis (RDA) using the CANOCO 4.5 software package, following Lepš and Šmilauer (2003). First a detrended correspondence analysis (DCA) was carried out on species distribution data only. The longest gradient was 2.35 SD (SD = standard deviation of units of species turnover), and therefore the species respond roughly linearly to gradients. Thus RDA was used following Lepš and Šmilauer (2003) for gradients less than 3 SD instead of CCA (canonical correspondence analysis), which is the appropriate model for a unimodal response.

RDA was carried out with a focus on inter-species correlation. Species scores were divided by the standard deviation. Additionally, species abundance data were log-transformed to prevent high values influencing the ordination. To evaluate environmental variables in their importance for determining

species data we used two consecutive approaches. In a separate model, environmental variables were treated individually, whereas variables were added sequentially into the model using a forward selection model (Monte Carlo permutation test with 1000 permutations under full model). Permutation restrictions were set to split-plot design (linear transect).

To extract the weight of single environmental factors, and to examine their relationship to the abundance of each species separately on the one hand and to the vigor-index score V on the other, we used multiple regression analyses, including stepwise forward procedures to exclude possible co-interactions.

To test for differences in canopy openness in transects within the two areas of differing disturbance history we used a Kruskal-Wallis one-way analysis of variance (ANOVA) on ranks including a Student-Newmann-Keuls all pairwise multiple comparison procedure.

RESULTS

Altogether we found 301 individuals of *S. lobeliaeformis*, 175 of *N. crassifolius* (including five individuals of the red-magenta-colored ecotype), and 75 individuals of *B. melancholica*, giving a total of 551 individuals of all investigated species in all transects covering a total area of 6000 m².

S. lobeliaeformis was most abundant in the upper transects (e.g. 65% of all individuals in T2 and T3), whereas abruptly in T4 only one individual was found, while in the lowest transects T5 and T6 the species was completely absent. *B. melancholica* showed a similar distribution pattern and was only present in higher elevations (T1, T2, and T3), with the highest number of individuals in the uppermost transect. *N. crassifolius* was concentrated in the lower regions (T4, T5, and T6) with only few individuals (including all five individuals of the red-magenta-colored ecotype) found at a higher elevation (T1 and T3).

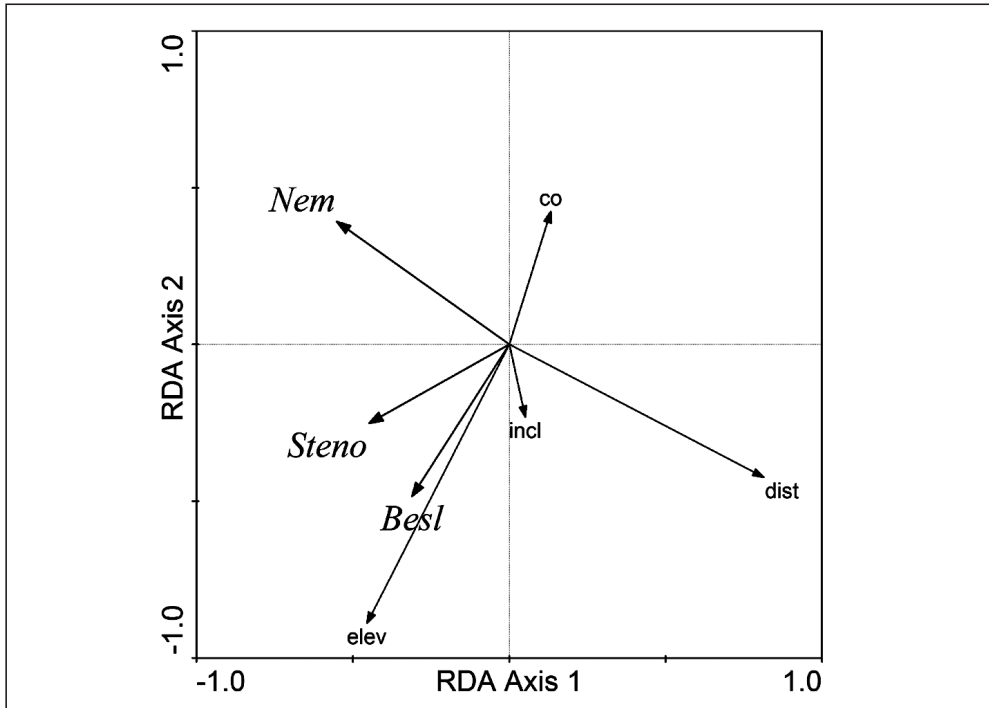


FIG. 2. RDA ordination diagram including all three species (*Steno* – *Stenostephanus lobeliaeformis*, *Besl* – *Besleria melancholica*, *Nem* – *Nematanthus crassifolius*; species fit range: 25–100%) and four environmental variables (elev – elevation, dist – distance to river, incl – inclination, and co – canopy openness).

The diagram indicates open habitats at low elevation near the river bank for *N. crassifolius* and more closed canopy conditions at higher elevation for *S. lobeliaeformis* and *B. melancholica*, both being more independent of proximity to the watercourse.

Distribution of all three species was explained mainly by elevation ($F = 12.48$, $P < 0.001$) and distance to river ($F = 11.65$, $P < 0.001$). We found minor and barely significant effects for inclination ($F = 3.01$, $P = 0.052$) and canopy openness ($F = 1.83$, $P = 0.227$). Altogether these four variables of the forward selection model explained 38% of the complete variance in species distribution. Exposure was completely excluded due to the lack of contribution to the model.

The ordination diagram emphasizes the considerable effects of the distance to the river in *N. crassifolius* as well as the influence of elevation on *S. lobeliaeformis* and *B. melancholica* within this model (Fig. 2).

The effect on abundance of various environmental factors differs between the investigated species (Table 2). Elevation was the only parameter significantly influencing the abundance of *S. lobeliaefor-*

mis, but the overall regression model is rather weak ($R^2 = 0.1$). Elevation had more influence on the abundance of *B. melancholica*, which was additionally affected by inclination. Both factors significantly contributed to the multiple regression model ($R^2 = 0.26$). *N. crassifolius* was almost exclusively found within proximate riparian vegetation. Therefore distance to the river was a crucial factor in *N. crassifolius*, whose abundance shows a negative correlation with this single parameter contributing to the multiple regression model ($R^2 = 0.23$). Neither canopy openness nor exposition had a detectable influence on the occurrence of the studied species (Table 2).

The effects of different environmental factors on vigor (using the vigor-index) also showed varying patterns between the species (Table 3). *S. lobeliaeformis* was the most sensitive species in terms of susceptibility to environmental influences. We observed a significant negative correlation with eleva-

TABLE 2. Results of a multiple regression analysis (stepwise forward) with influence of environmental variables on abundance.

group	<i>S. lobeliaeformis</i>				<i>B. melancholica</i>				<i>N. crassifolius</i>			
	std. coeff.	R	F	P	std. coeff.	R	F	P	std. coeff.	R	F	P
canopy openness	-		0.027	0.871	-		0.430	0.515	-		2.104	0.152
distance to river	-		2.337	0.132	-		0.140	0.710	-	0.474	16.514	<0.001
easterness	-		0.131	0.719	-		0.592	0.445	-		0.007	0.935
elevation	0.312	0.312	6.146	0.016	0.408	0.445	12.382	<0.001	-		1.951	0.168
inclination	-		0.754	0.389	0.259	0.514	4.984	0.03	-		1.178	0.282
R²	0.1				0.26				0.23			

tion and a positive one with canopy openness relating to the vigor of this species, resulting in a multiple regression coefficient of $R^2 = 0.36$. In contrast, *B. melancholica* was very robust regarding the influence of the environmental gradients on vigor. There was no significant effect of any tested parameter at all in this species. The vigor of the epiphytic *N. crassifolius* showed a significant positive response to canopy openness only, but overall the regression model was weak ($R^2 = 0.05$).

Canopy structure between the upper (T1, T2, and T3) and lower transects (T4, T5, and T6) differed: canopy openness in the lower transects within the formerly clear-cut area is significantly higher than in the upper transects within the area where selective logging took place (Table 4).

DISCUSSION

The distribution of the chosen species in this study is mainly influenced by elevation and distance to the river. Both factors stand for variation in microclimatic habitat conditions (temperature, wind, and evapotranspiration). Vigor data of understory plants based on growth variables seem to be more sensitive and responsive to such small-scale environmental

gradients. Therefore more qualitative information on ecological requirements and logging disturbances should be obtained.

S. lobeliaeformis and *B. melancholica* are abundant in transects at the higher elevation and completely absent in the two lowest ones, whereas *N. crassifolius* is common in this lower region only. The complete altitudinal gradient amounts to only 207 m, and is completely situated in the submontane level within a forest formation subjected to differing extents of logging activity in the past. There are considerable relationships between environmental gradients and both abundance and vigor of the studied species within such a small-scale region. Similar results have been published for Cyclanthaceae (Freiberg & Gottsberger 2001), for other herbaceous plants (Horvitz & Le Corff 1993), as well as for lianas and trees (Liebermann *et al.* 1985).

N. crassifolius occurs mainly in the lower part of the research area and almost exclusively directly by the river. This confirms the observations of Lopes *et al.* (2005). Epiphytes have no access to soil water and rely on air humidity and precipitation. The humus layer on the phorophyte can provide limited water resources, but epiphytic species can fall back only on

TABLE 3. Results of a multiple regression analysis (stepwise forward) with influence of environmental variables on vigor-index score.

group	<i>S. lobeliaeformis</i>				<i>B. melancholica</i>				<i>N. crassifolius</i>			
	std. coeff.	R	F	P	std. coeff.	R	F	P	std. coeff.	R	F	P
canopy openness	0.226	0.352	9.669	0.002	-		1.205	0.234	0.227	0.227	9.184	0.003
distance to river	-		0.740	0.390	-		-1.107	0.274	-		1.771	0.185
easterness	-		3.522	0.062	-		-0.242	0.810	-		0.003	0.959
elevation	-0.460	0.309	40.016	<0.001	-		0.472	0.639	-		0.740	0.391
inclination	-		0.363	0.548	-		-0.574	0.569	-		2.807	0.096
R²	0.36				0				0.05			

TABLE 4. Results of a Kruskal-Wallis one-way ANOVA on ranks including a Student-Newmann-Keuls all pairwise multiple comparison procedure of canopy openness conditions in two forest formations with different disturbance history.

group	<i>N</i>	median	25%	75%
selective cut	30	6.87	6.58	7.5
Clear-cutting	30	7.93	7.39	8.89

$H = 12.909$; $df = 1$; $P < 0.001$
 selective logging vs. clear-cutting: diff of ranks = 486;
 $q = 5.081$; $P < 0.05$

water stored within their own plant body if such sources are depleted (Freiberg 2000, Freiberg & Gottsberger 2001). Therefore *N. crassifolius* depends on habitats with adequate air humidity. In addition, pollination and dispersal may be explanations for the population structure of *N. crassifolius*. Pollination rates are possibly higher along the riverbanks, given the accumulation of individuals and a better accessibility for pollinators. Based on the flowering pattern it is probable that hummingbirds are the main pollination agents. Higher pollination rates go along with higher fructification rates. The fruits of *N. crassifolius* are fleshy capsules and dispersal by birds is likely. Birds mostly prefer open corridors like rivers and defecate in the immediate vicinity (Charles-Dominique 1986), resulting in a concentration of *N. crassifolius* near riversides and isolated individuals within the forest interior (Lopes *et al.* 2005). There is no empirical information about any causality between reproduction rate, seed dispersal, and population structure in *N. crassifolius*, therefore any argumentation is hypothetical.

The vigor performance of *N. crassifolius* shows a significant but rather weak positive correlation with canopy openness (Table 3). Light availability is known to be the main determinant of the vertical distribution of epiphytes on host trees (Wolf 1994) and might be an important parameter here. But if air humidity is at a constantly high level, relative irradiance is only a secondary limiting factor for growing power.

S. lobeliaeformis and *B. melancholica* occur synoptically in the upper transects. Nevertheless they were barely found together within the same plot. It is expected that both species have similar habitat requirements, but avoid strong competition by using different niches provided by the multifarious riverine

microhabitats. Even small-scale topographic differences influence edaphic and hydrological conditions, leading to such habitat diversity (Austin & Greig-Smith 1968, Williams *et al.* 1969, Hall and Swaine 1981). The genus *Besleria* is known to be common on steep slopes at medium elevations in the Atlantic Forest (Lopes *et al.* 2005, Chautems, pers. comm.), which was confirmed for *B. melancholica* in this study by the positive relationship between abundance and elevation as well as inclination. Steep slopes are well aerated via lateral runoff, whereas water accumulates in hollows. *B. melancholica* seems to rely on well-drained soils for establishment and represents an example of the influence of complex microtopographical gradients on species distribution within heterogeneous microhabitats (Webb 1968). Regarding to our study *B. melancholica* is a generalist species, underlined by the evidence of no significant effects on the vigor performance (Table 3).

On the other hand more substantial effects were recorded for *S. lobeliaeformis*. We registered an abrupt disappearance of *S. lobeliaeformis* after a constant increase in vigor performance with decreasing elevation. This inconsistent finding may be caused by the different disturbance history in this region (Fig. 3). The borderline of the range of *S. lobeliaeformis* is consistent with this pattern. In the lower part of this area where clear-cutting took place in the 1940s the species is completely absent, whereas in the upper region only selective logging was conducted before the 1970s (Locke, pers. comm.). It is presumed that *S. lobeliaeformis* normally occurs in the lower area and performs better there than in higher regions. The responsible factor could not be isolated but it seems certain that there is some kind of distribution barrier for *S. lobeliaeformis* which might be due to the different disturbance history. The antithetical finding of increasing abundance with increasing elevation (Table 2) can be neutralized by removing all plots with no individuals of *S. lobeliaeformis* or removing all plots with a history of severe logging from the analysis. After both modifications no environmental parameter has any significant influence on the abundance of that species. A prospective approach on a larger scale, including the extension of the altitudinal gradient, could be helpful at this point. Another indication for the hypothesis that *S. lobeliaeformis* responds to modified conditions according to differing logging impact is the different forest structure. Canopy openness of the lower transects within the former clear-cutting area is significantly higher than in the upper transects within the area where selective

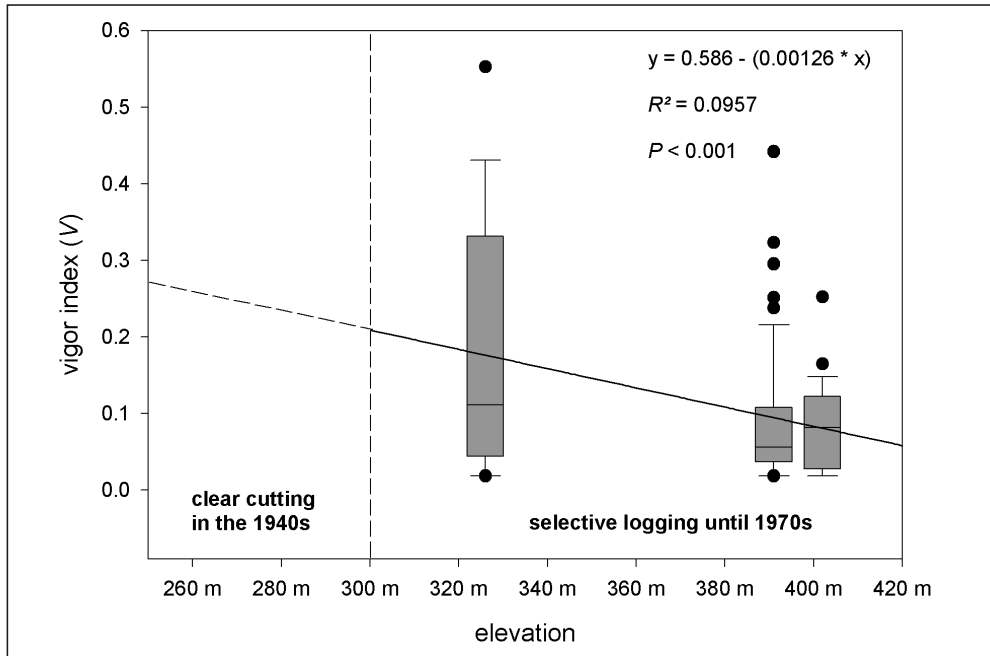


FIG. 3. Significant trend in decrease of vigor in *Stenostephanus lobeliaeformis* with increasing elevation. The species was found only in the three upper transects and was absent in the lower ones. The distribution pattern agrees with the range of different logging activities of the particular areas.

logging took place (Table 4), and canopy openness was identified as positively influencing the vigor of *S. lobeliaeformis* as well (Table 3). But this finding has to be accepted with reservations because of the co-correlation between canopy openness and elevation ($r = -0.437$, $P < 0.001$) and the location of the areas with different disturbance histories at different altitudinal levels. Thus we cannot certainly distinguish between the influence of elevation and historical use of the area.

Although this study only deals with three representative understorey species, in summary the influence of complex environmental gradients on abundance and vigor is observable, even on a small-scale level. Apparently there are differences within a small altitudinal range and within the same vegetation formation and our results may be applicable to the whole understorey community (Drucker *et al.* 2008). Apart from the different ecological requirements of the species, a potential impact of past logging activities on abundance and vigor cannot be denied. Generally the high sensibility of certain species to environmental changes due to land use activities

might be useful as an indication tool for management issues in areas with different disturbance histories. The vigor-index introduced within our study has been proved helpful for detecting growth responses due to changing environmental conditions. Biomass could also be an appropriate factor to ascertain the level of vigor (Freiberg & Gottsberger 2001), but lacks the advantage of being non-destructive.

ACKNOWLEDGMENTS

We are grateful to the “Reserva Ecológica de Guapiçu” (REGUA) and the whole staff, especially to Mr. Nicholas Locke, for logistical support and the permission to work on the property. We would like to thank Alain Chautems and an anonymous reviewer for helpful comments on the manuscript. For field assistance we would like to thank Corinna Burkart and Maria Faske, as well as Dietmar Sattler for valuable help in preparing this study and providing mobility backup in arduous conditions. We are grateful to the University of Leipzig and the German Academic Exchange Service (DAAD) for funding.

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