

1 **Sprouting extends the regeneration niche in temperate rain forests: The case of the**  
2 **long-lived tree *Eucryphia cordifolia*.**

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32 **ABSTRACT**

33 Sprouting is a widespread trait of geographical, ecological and taxonomical scales that  
34 allows resource exploitation, space colonization, vegetative reproduction and post-  
35 disturbance persistence. It is considered that persistence is the most frequent functional role  
36 of sprouting in woody plants. Here we propose that niche differentiation between sprouts  
37 and saplings extends the regeneration niche to suboptimal conditions for sexual  
38 recruitment. To test this hypothesis, we sampled root suckers (sprouts) and saplings of the  
39 long-lived tree species *Eucryphia cordifolia* Cav. in an even-aged coastal temperate rain  
40 forest. Canopy openness was measured over each recruit as a proxy of regeneration niche.  
41 Sapling survival was checked after two years. The entire forest canopy openness range was  
42 used as an estimation of niche availability. Light and microclimatic conditions were  
43 recorded for different canopy openness. Sprouts and saplings occupied a narrow range of  
44 the canopy openness near to the closest extreme of the gradient (4.8-14.1%). The  
45 distribution of saplings was explained by the lower survival of small saplings under more  
46 open canopies, as a consequence of the interactive effect of higher evaporative demand and  
47 radiation load in more opened canopies. Although the niches of sexual and vegetative  
48 recruits slightly overlap (31% of the interquartile range on average), sprouts inhabit the  
49 more opened sites. Therefore, sprouts extend the regeneration niche to suboptimal  
50 conditions for sapling establishment. Our results contribute towards explaining the high  
51 colonization ability of *E. cordifolia* in this kind of forest, whose composition is strongly  
52 driven by gap dynamics.

53

54 **Highlights:**

- 55 • Saplings and sprouts of *Eucryphia cordifolia* show niche selection
- 56 • Sapling survival is driven by the interactive stress of drought and high irradiance
- 57 • Niche differentiation between sprouts and saplings extends the regeneration niche

58

59 **Keywords:** Niche breadth, root suckers, gap colonization, sapling survival, interactive  
60 abiotic stress

## 61 **1. Introduction**

62 Sprouting is a widespread, ancestral trait, appearing in a wide range of ecosystems and  
63 lineages (Wells, 1969; del Tredici, 2001; Bond and Migdley, 2003; Vesk and Westoby,  
64 2004). The very high frequency of sprouting at both ecological and taxonomical scales  
65 reflects its functional diversity (van Groenendael et al., 1996; del Tredici, 2001); it allows  
66 populations: (1) to exploit resources when they are scarce or heterogeneously distributed in  
67 the space (exploitation function); (2) to increase the competitive ability by fast colonization  
68 of gaps in high productive ecosystems (colonization function); (3) to increase reproduction  
69 in stressful environments or in species with low sexual reproductive success (reproduction  
70 function); and (4) to regenerate vegetatively after disturbances of different severities (i.e.  
71 resprouting *sensu* Clarke et al., 2013; persistence function). It is considered that clonal  
72 growth in herbaceous species mostly allows gathering resources, space colonization and  
73 reproduction, whereas the primary benefit of sprouting for woody species is recovering  
74 after disturbances (Peterson and Jones, 1997). In fact, resprouting is a cornerstone trait  
75 determining resilience to disturbances in woody plant communities (Keeley, 1986; Bond  
76 and Migdley, 2001).

77 In ecosystems under a low-severity disturbance regime, sprouting of woody plants  
78 occurs in the absence of major disturbances, suggesting other functional meanings of  
79 sprouting (Jeník, 1994; Peterson and Jones, 1997). For instance, clonal growth by spreading  
80 non-splitting sprouts is frequent in stressful environments such as marsh wetlands or tree-  
81 lines (Pennings and Callaway, 2000; Peltzer, 2002). The subsidy of water, sugars and  
82 nutrients from parent plants increases the chance of survival of non-splitting sprouts under  
83 abiotic stressful conditions (Wiehle et al., 2009). In the high productive rain forests,  
84 competition induces biotic stress and strongly determines species assemblage (Kraft et al.,  
85 2008). In these ecosystems, woody plants show almost all forms of sprouting and most of  
86 them increase colonization rates and thus competitive ability (Grubb, 1987; Jeník, 1994).

87 Opportunities of colonization in rain forests mainly occur after canopy openness,  
88 such as tree-fall gap formations (Denslow, 1987). Commonly, sexual regeneration is in  
89 competitive disadvantage against sprouts due to their lower growth rates during early  
90 developmental stages (Farahat and Lechowicz, 2013). This is exacerbated in gaps where  
91 microsite conditions are likely to become unsuitable for seedling establishment. The

92 interaction between the sudden increment of high irradiance and subsequent evaporative  
93 demand in gaps might lead to some level of drought (Tognetti et al., 1994; Flexas et al.,  
94 1999). This is especially true for shade saplings, which present several traits towards the  
95 maximization of light capture, which are antagonistic to those described for water stress  
96 resistance, resulting in an exacerbated water stress sensibility (Valladares and Pearcy,  
97 2002). In these cases, sprouts would extend the regeneration niche to suboptimal conditions  
98 where the chance of sexual recruitment is low.

99         The regenerative dynamics of the coastal temperate rain forest of south-central  
100 Chile is strongly driven by the occurrence of individual tree-fall gaps, which increases  
101 environmental heterogeneity, thus allowing the coexistence of different plant functional  
102 types (e.g. Armesto and Fuentes, 1988; Gutiérrez et al., 2008). Specifically, gaps are  
103 suitable for the seedling establishment of shade-intolerant species, whose survival is  
104 negligible in deep shaded microsites because the low carbon gain induces carbon starvation  
105 (Givnish, 1988). For intermediate shade-intolerant species, such as the long-lived tree  
106 species *Eucryphia cordifolia* Cav., small gaps seem to be adequate for sexual recruitment  
107 (Lusk et al., 2006; Gutiérrez et al., 2008). This species produces high amounts of viable  
108 seeds from an early age onwards, which can be dispersed over long distances (Escobar et  
109 al., 2006). Although germination is usually greater in understory conditions, it is not  
110 negligible in gaps (Figueroa and Lusk, 2001). Therefore, the spatial pattern of sexual  
111 recruitment of *E. cordifolia* (i.e. at intermediate canopy openness) is not explained by seed  
112 availability and germination but by seedling establishment and survival. In fact, although  
113 seedlings of this species have been recorded immediately after gap formation, most of them  
114 fail to survive after two years (González et al., 2002). In addition to sexual recruitment, this  
115 species profusely sprouts from roots, even in the absence of disturbances; contrary to sexual  
116 recruits, root suckers show very low mortality (Donoso et al., 1985; Veblen, 1985;  
117 González et al., 2002). The coexistence of the two regeneration mechanisms in *E.*  
118 *cordifolia* and gap dynamics of the coastal temperate rain forest provides an excellent  
119 model to evaluate the role of sprouting in extending the niche regeneration to limiting  
120 conditions for sexual recruitment. To test this hypothesis, we addressed the following  
121 questions: (1) does niche selection exist in sprouts and saplings of *E. cordifolia*?; (2) which  
122 environmental condition constrains the survival of *E. cordifolia* saplings?; (3) does niche

123 differentiation between sprouts and saplings extend the niche regeneration? In order to  
124 fulfill these aims, we considered the canopy openness as a proxy of ecological niche, since  
125 it involves the availability of key resources like light and water (Brown, 1993; Maherali et  
126 al., 1997).

127

## 128 **2. Material and methods**

### 129 *2.1. Study site*

130 This study was conducted during the growing seasons of 2011 to 2013 in a 30 ha secondary  
131 coastal temperate rain forest located in south-central Chile (Katalapi Park: 41°31'8" S,  
132 72°45'2" W, elevation ca. 90 m a.s.l.). The forest structure corresponds to ca. 35 year old  
133 even-age forest where the taller individuals reach up to 10 m, but with some old-growth  
134 remnant trees. The study site presents several open areas previously used for cattle  
135 activities. For the last 27 years, the forest has been protected from anthropogenic alterations  
136 (logging, cattle), allowing for regeneration of both sun and shade species. The most  
137 frequent tree species are *Nothofagus nitida* (Phill.) Krasser, *Nothofagus dombeyi* (Mirb.)  
138 Oerst, *Laureliopsis philippiana* (Looser) Schodde, *Aextoxicum punctatum* R. et P.,  
139 *Eucryphia cordifolia* Cav., *Drimys winteri* J.R. et G. Forster, and several Mirtaceae  
140 (Saldaña et al., 2005; Lusk and Corcuera, 2011; Coopman et al., 2011).

141 This area presents a maritime temperate climate, with annual rainfall of ca. 1900  
142 mm concentrated between April to November (ca. 77% annual rainfall; data from 1861 to  
143 2001; Tepual Airport weather station: 41° 25' S, 73° 05' 85" W; Meteorological Office of  
144 Chile, <http://www.meteochile.gob.cl/>) and a mild dry season during December to March. In  
145 this period, the mean air temperature reaches 15° C, the lowest air relative humidity range  
146 between 45-55% and a 15-day-long dry period frequently occurs within each summer.  
147 Climatic details for the study area are shown in Coopman et al. (2010).

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### 149 *2.2. Forest canopy openness*

150 The forest canopy openness gradient was determined on 8 transects 100 m long on average  
151 randomly distributed along the forest. To ensure that we included the entire light gradient,  
152 transects were started in open sites located at the edge of the forest and continued through  
153 the closed forest. Hemispherical photography was used to measure canopy openness

154 (Chazdon and Field, 1987) by using a Coolpix 4500 digital camera equipped with a FC-E8  
155 fisheye lens (Nikon, Tokyo, JP). A photograph was captured at 5 m intervals along each  
156 transect at 40-60 cm height, resulting in a total of 161 photographs. The camera was hand  
157 leveled and oriented so that the top of the image faced north. Photographs were taken on  
158 homogeneous overcast days. The resulting photographs were analyzed for the percentage of  
159 canopy openness (hereafter CO) with the Gap Light Analyzer 2.0 software (GLA; Frazer et  
160 al., 1999).

161

### 162 2.3. Canopy openness and microsite environment

163 To relate CO with microsite conditions we recorded photosynthetic photon flux density  
164 (PPFD), air temperature (Ta) and relative humidity (RH) at different CO ranging from 2 to  
165 100% (see Fig. 1). In the open site (100% CO), we used a Li-1400 data logger connected to  
166 LI250, LI 1400-104 and LI 1400-106 sensors (Li-Cor Inc., NE., USA). For measurements  
167 inside the forest, we installed H21-002 HOBO meteorological stations connected to S-LIA-  
168 M003 and S-THA-M0xx sensors (Onset, MA, USA). Data were recorded at 30 minute  
169 intervals from 2007 until 2013 (except 2010 due to technical troubles). The air vapor  
170 pressure deficit (VPD) was determined according to Murray (1967):

171

$$172 \text{ VPD} = P_v - ((\text{RH}/100) * P_v),$$

173 where  $P_v$  is calculated as follows:

$$174 P_v = 0.611 \exp [17.27 \text{ Ta}/(\text{Ta} + 237.3)].$$

175

### 176 2.4. Regeneration niche

177 More than 90% of the surface area of the forest was inspected looking for saplings.  
178 Regarding sprouts, previous observations indicated that they only appear close to mature  
179 trees. Therefore, sprouts were recorded in 15 plots of 200 m<sup>2</sup> established around mature  
180 trees, in such a way each plot covered a wide range of canopy openness (i.e. from big gaps  
181 to closed forest). *Eucryphia cordifolia* sprouts from the root collar and from roots (root  
182 suckers; e.g., Veblen 1985). However, for the aim of this study, we only sampled root  
183 suckers, because basal sprouts are generally associated to severe damage (persistence  
184 function; Jeník, 1994). Sampled recruits were taller than 2 cm in height but shorter than 175

185 cm. We excluded older recruits (i.e. taller), because environmental conditions at the  
186 establishment time would have been different to current conditions. Each plant was  
187 carefully inspected and recognized as originating from sprout or seed. Specifically, recruits  
188 were identified as sprouts when they showed a “T-inverse” at the underground level,  
189 meanwhile saplings did not show any subsidiary root connection or root scar indicating past  
190 connections. A hemispherical photograph over plant apex was recorded (see section 2.2 for  
191 details). If recruits were clustered and the canopy structure was homogeneous over them,  
192 one photograph was taken directly above the group of recruits. Because the sensitivity of  
193 woody plants to environmental conditions changes with the ontogeny (Coopman et al.,  
194 2008), the height of both sprouts and saplings was measured. All saplings, except 50 (that  
195 were harvested in a parallel study), were tagged to check survival two years later (March  
196 2013). A sapling was considered dead when the above-ground biomass was totally  
197 necrosed or when no leaves or axillaries buds were observed on the stem.

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### 199 *2.5. Statistical analyses*

200 For each CO, we calculated daily (from 7:00 to 19:00 h) 90% percentile of PPF and VPD.  
201 We used percentile instead maximum and minimum values to avoid extreme (non-frequent)  
202 conditions. Then, the percentiles were averaged for each summer period (i.e. December to  
203 February) and independently correlated with CO. After visual inspection, linear regression  
204 was tested for VPD, whereas logistic regression was used in case of PPF. Because most  
205 measurements were concentrated in the closed end of the canopy openness gradient, we  
206 log-transformed this variable.

207 Niche selection was evaluated by comparing the distribution of the CO for each  
208 recruit type with those of the forest by means of the Kolmogorov-Smirnov test. Because we  
209 were aware that sampling design would bias the distribution of the forest CO towards the  
210 upper extreme of the gradient, we repeated the analyses excluding those CO values higher  
211 than 31.4% which corresponded to the 75% quantile of the forest. In addition, we  
212 conducted similar analyses comparing independently the distribution of forest CO with that  
213 of recruits of different height classes defined on the quartile basis. Height classes were  
214 established separately for sprouts and saplings to ensure a large enough sample size for  
215 each recruit type and height class.

216 Changes of the sapling survival probability along the light availability gradient and plant  
217 height were analyzed by means of Generalized Linear Model (GLM), assuming a binomial  
218 distribution error and logit link function, and tested by an analysis of deviance (McCullagh  
219 and Nelder, 1989). Because of the high skewness of the distribution of saplings towards the  
220 shaded extreme of the gradient (Fig. 2), differences in survival under low light availability  
221 would be difficult to detect with raw data. Therefore, CO was divided into quartiles, and  
222 differences in survival tested among CO classes. Plant height classes were defined in the  
223 same way and included as independent variable in the model. Because the analysis of  
224 survival was conducted with a subset of the initial saplings (see section 2.4.), height classes  
225 slightly differed from those established in the evaluation of niche selection (see Table 1 and  
226 Figure 3). The canopy openness and sapling height distributions for this subset did not  
227 significantly differ from those of the initial set of saplings ( $P = 0.828$  and  $P = 0.398$   
228 respectively in the Kolmogorov-Smirnov test).

229         Comparison of the mean CO between sprouts and saplings was performed by means  
230 of permutational ANOVA (PERMANOVA; Anderson, 2001). This statistical tool was  
231 chosen because the response variable was not normal and any transformation corrected this  
232 issue. PERMANOVA analysis was conducted based on 10,000 permutations with the  
233 function *adonis* of the library *vegan* of the R program (Oksanen, 2011). This function is  
234 less sensitive to differences in the dispersion between groups than other sister functions  
235 (Oksanen, 2011).

236         To evaluate niche overlap between the two types of recruits, the first and third  
237 quartiles of CO for both sprouts and saplings were calculated. Then, the 95% confidence  
238 intervals of the quartiles were estimated by bootstrapping ( $n = 10,000$ ). They were  
239 considered significantly different when the proportional overlap of the confidence interval  
240 was less than 0.5 (Cumming, 2009). Finally, in order to evaluate if sprouts increase niche  
241 breadth, we calculated the Levins' index for saplings and saplings+sprouts according to  
242 Colwell and Futuyma (1971). This index has been suitable for assessing niche breadth in  
243 the CO dimension in temperate rain forests (Saldaña et al., 2005). The 95% confidence  
244 intervals of the Levins' indexes were estimated by bootstrapping ( $n = 10,000$ ) and the  
245 proportional overlap calculated to test for differences between saplings and  
246 saplings+sprouts.

247 **3. Results**

248 Canopy openness (CO) and photosynthetic photon flux density (PPFD) were related in a  
249 threshold fashion, in such a way that PPFD abruptly increases from 10% CO (Fig. 1a).  
250 Accordingly, vapor deficit pressure (VDP) was positively correlated with CO (Fig. 1b).

251 The Kolmogorov-Smirnov test indicates that neither sprouts nor saplings are  
252 randomly distributed along the CO gradient of the study area ( $P < 0.001$  in both cases;  
253 Table 1). Similar results were obtained when the higher CO values were excluded from the  
254 analyses (i.e., higher than the 75% quantile of the forest CO;  $P < 0.001$ ), indicating that such  
255 differences were not due to the long tail of the distribution of forest CO, and thus to a  
256 possible bias in the sampling design. However, whereas the distribution of CO for the  
257 forest was mesokurtic (kurtosis = 0.23;  $P = 0.280$ ), the distribution of CO for sprouts and  
258 especially for saplings was leptokurtic (kurtosis = 3.82, kurtosis = 16.85 respectively;  $P <$   
259  $0.001$  in both cases), indicating that most recruits were concentrated around the  
260 corresponding mean values of CO (Fig. 2). The fact that sprouts were rare in very open  
261 sites supports our assumption that they were not related to disturbances. When comparisons  
262 were conducted independently for each height class, we found that the CO distribution of  
263 sprouts significantly differed with that of the forest for all height classes except for sprouts  
264 between 6 and 35 cm in height (Table 1). For saplings, we found significant differences in  
265 the CO distributions for all height sapling classes except for the tallest one (Table 1).

266 Survival probability increases with sapling height, but no differences were detected  
267 among CO classes (Table 2). However, when the tallest plants were excluded from the  
268 analysis, differences between CO classes emerged, with sapling survival higher in closed  
269 sites (Table 2, Fig. 3); differences between height classes remained significant in this last  
270 analysis (Table 2).

271 The upper quartile of the CO of saplings (9.2%; bootstrapping confidence interval:  
272 [5.2, 11.3]) significantly overpassed the lower quartile for sprouts (7.6%; bootstrapping  
273 confidence interval: [7.0, 13.4]). However, the interquartile ranges of the two recruits only  
274 overlapped in a 31% on average (25% of the interquartile range of sprouts and 38% for  
275 saplings; see ranges in the Figure 1 caption). Accordingly, PERMANOVA analyses  
276 detected significant differences in CO between sprouts and saplings (Table 3). Specifically,  
277 saplings were found, on average, at more closed sites than sprouts. Consequently, the

278 Levins' index for saplings ( $B = 0.58$ ; bootstrapping confidence interval: [0.52, 0.63]) was  
279 significantly lower than the index for saplings+sprouts ( $B = 0.70$ ; bootstrapping confidence  
280 interval: [0.66,0.73]).

281

#### 282 **4. Discussion**

283 Sprouting as a reproductive strategy commonly occurs in stressful environments where  
284 seedling establishment is negligible (van Groenendael et al., 1996). However, sprouting  
285 under suboptimal environmental conditions for sexual recruitment would be an advantage  
286 through regeneration niche extension. This is the case of the long-lived pioneer tree species  
287 *Eucryphia cordifolia*, which has yearly sexual recruitment non-randomly distributed in the  
288 forest (Escobar et al., 2006 and this study). The range of canopy openness (CO) occupied  
289 by *E. cordifolia* saplings was narrower than the entire CO gradient available in the forest,  
290 and concentrated in the shadiest portion (4.8-9.2% CO; Fig. 2), thus reflecting niche  
291 selection (Table 1). Sprouts also select for the closed end of the CO gradient (7.6-14.1%  
292 CO; Table 1, Fig. 2). Because CO ranges of sprouts and saplings do not fully overlap, the  
293 regeneration niche is wider when both recruit types are pooled together, instead of  
294 considering saplings alone. This extended regeneration niche likely explains why *E.*  
295 *cordifolia* is frequently considered an emergent species (Escobar et al., 2006) despite the  
296 higher frequency of saplings in closed sites.

297         The fact that both sprouts and saplings recruit near to the closest extreme of CO  
298 gradient could have different explanations. Shady habitats of sprouts are likely due to the  
299 spatial association with the parent plant and not to environmental constraints, since juvenile  
300 non-splitting sprouts are subsided by parent plants (Oborny et al., 2000; Wiehle et al.,  
301 2009). On the contrary, saplings would maintain a higher dependency to environmental  
302 conditions. In this sense, the scarcity of saplings recruiting at CO lower than 5% is likely  
303 determined by high mortality at light intensities below their light compensation point (LCP  
304  $= 5.3 \pm 1.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; Fig. A1 supplementary data). Usually more than half of daily  $\text{CO}_2$   
305 uptake is lost in respiratory processes necessary for growth and maintenance (Turnbull et  
306 al., 2001; Flexas et al., 2006). Consequently, these quite similar LCP and midday PPFD  
307 availability ( $7.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ : 90% percentile of daily PPFD at 5% CO), mean that the  
308 daily-based carbon balance is severely restricted, reaching frequently negative values. In

309 agreement with our findings, a high mortality of *E. cordifolia* seedlings has also been  
310 reported by Lusk and Del Pozo (2002) at similar low light intensity ( $12 \mu\text{mol m}^{-2}\text{s}^{-1}$ ).

311 At the other extreme of the CO gradient (i.e., more open sites), both irradiance and  
312 evaporative demand increases (Fig. 1). The prevailing rainfall regime induces low VPDs  
313 during the beginning of the growing season. This allows seedling survival regardless of  
314 CO, despite their small and shallow rooting systems, commonly developed into the highly  
315 porous litter. In summer, the interaction of increased VPD and the abrupt rise of midday  
316 PPFDs from 10% CO would generate water stress (Fig. 1A). During periods of insufficient  
317 water supply, the otherwise beneficial light conditions become excessive because of  
318 reduced carbon assimilation. This imbalance leads to photoinhibition and photooxidative  
319 stress (Flexas et al., 1999). Consequently, environmental conditions might become critical  
320 during the short dry periods in summer (see section 2.1) and likely explains the mortality of  
321 small saplings at more open sites (Fig. 3). Accordingly, survival of large saplings (29-155  
322 cm in height) were affected by CO (Table 1 and 2, Fig. 3), possible because their root  
323 systems are able to supply water requirements even at more open sites.

324 Tree-fall gap formation is a key process driving vegetation dynamics and  
325 composition in coastal temperate rain forests (Gutiérrez et al., 2008). The role of advance  
326 (i.e., pre-disturbance) regeneration to refill gaps is well established (Denslow 1987 and  
327 references therein). In this regard, the extended regeneration niche of *E. cordifolia*  
328 improves its competitive ability within forest gaps. In fact, the fast gap colonization of *E.*  
329 *cordifolia* is not only due to its capacity to reoccupy their own gaps (i.e. resprouting),  
330 which are quite frequent in temperate rain forests (Gutiérrez et al., 2008), but also to growth  
331 stimulation of pre-disturbance sprouts in response to gap formation (González et al., 2002).  
332 In this sense, pre-disturbance sprouts might function as a suppressed sapling bank (*sensu*  
333 Grime, 1979), able to grow and reach maturity when conditions become favorable (e.g.  
334 gaps), but become suboptimal for sexual regeneration.

335 Here, we provide new knowledge on sprouting ecology that also reveals important  
336 implications for forest management. *Eucryphia cordifolia* is an economically promising  
337 tree species, due to its fast growth, its highly appreciated wood, and the melliferous quality  
338 of its flowers. The high mortality of saplings under the prevailing light and water  
339 availabilities of opened canopies will be exacerbated in the study area under the predicted

340 40% decline in summer precipitation over the next 70 years (Fuenzalida et al., 2006;  
341 Solomon et al., 2007). In this scenario, current fail of sexual recruitment would be  
342 exacerbated and forest regeneration dominated by clonal growth, leading to a reduction in  
343 the genetic diversity with the aforementioned endogamous depression and susceptibility to  
344 pathogens (Honnay and Bossuyt, 2005). Our results also highlight the relevance to  
345 distinguish between vegetative and sexual recruitment in relation to shade-tolerance and  
346 longevity, which are cornerstone considerations in regeneration dynamics studies and forest  
347 management (Valladares and Niinemets, 2008).

348

## 349 **5. Conclusions**

350 *Eucryphia cordifolia* saplings show niche selection, which is modulated by the differential  
351 survival of small plants along forest environmental gradients. Sapling survival is mainly  
352 driven by the interactive effect of water stress and high irradiance. Sprouting allows  
353 regeneration of *E. cordifolia* under suboptimal conditions for sexual recruitment, expanding  
354 its niche regeneration.

355

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363

## 364 **Appendix A. Supplementary data**

365 Fig. A1. Light-response curve of *E. cordifolia* saplings.

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507 **Figure captions**

508

509 Fig. 1. Changes in the 90 percentile of daily (from 7:00 to 19:00 h) photosynthetic photon  
510 flux density (PPFD) and vapor pressure deficit (VPD) along the canopy openness gradient  
511 for the study area in summer (December to February). Discontinuous lines represent fitted  
512 models: logistic for PPFD ( $R^2 = 0.99$ ) and linear for VPD ( $R^2 = 0.35$ ). The estimated PPFD  
513 at 5% of canopy openness ( $7.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) is quite similar to the light compensation point  
514 (LCP) of *E. cordifolia* saplings ( $5.3 \pm 1.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). Notice the absence of VPD values  
515 at 10% of canopy openness due to erroneous humidity data logging.

516

517 Fig. 2. Canopy openness distribution of *E. cordifolia* sprouts, saplings and the forest in the  
518 study area. Interquartile ranges of canopy openness were 7.6-14.1, 4.8-9.2 and 4.9-31.4%,  
519 respectively.

520

521 Fig. 3. Percent of survival of *E. cordifolia* saplings for each canopy openness and height  
522 classes. Height classes were defined on the quartile basis. For canopy openness classes, the  
523 value of the upper limit of each class is indicated. Symbols indicate the mean survival for  
524 each height classes regardless of the canopy openness. The sample size for each  
525 combination of canopy openness and height classes is indicated over the corresponding bar.  
526 Notice that height classes slightly differ from the height classes shown in Table 1 (see  
527 detail in the main text).

528

529

**Sprouting extends the regeneration niche in temperate rain forests: The case of the long-lived tree *Eucryphia cordifolia*.**

**Highlights:**

- Saplings and sprouts of *Eucryphia cordifolia* show niche selection
- Sapling survival is driven by the interactive stress of drought and high irradiance
- Niche differentiation between sprouts and saplings extends the regeneration niche

Table 1. *P*-values of the Kolmogorov-Smirnov tests comparing canopy openness distribution between the forest and each recruit type (sprouts and saplings) of *Eucryphia cordifolia*. Analyses were conducted pooling all height classes and independently for each height class.

Height class	Sprouts			Saplings		
	Height (cm)	n	<i>P</i> -value	Height (cm)	n	<i>P</i> -value
All	6-164	297	<0.001	2-155	219	<0.001
Very small	6-35	74	0.488	2-9	55	0.012
Small	35-53	76	0.002	9-16	55	<0.001
Intermediate	53-87	73	0.035	16-30	58	0.028
Large	87-164	74	<0.001	30-155	51	0.089

Table 2. Analysis of deviance for the probability of *E. cordifolia* sapling survival with canopy openness (CO) and heights (H) classes.

Trait	Df	Deviance	Residual Df	Residual Deviance	P-value
<i>All height classes</i>					
Null			168	232.14	
CO	3	5.85	165	226.30	0.119
H	3	10.90	162	215.39	0.012
CO x H	9	5.81	153	209.58	0.759
Overdispersion		1.38			
<i>75% smallest heights</i>					
Null			127	172.92	
CO	3	9.03	124	163.89	0.029
Height	2	8.10	122	155.79	0.017
CO x Height	6	2.14	116	153.66	0.907
Overdispersion		1.36			

Table 3. Results of the PERMANOVA analysis comparing the mean canopy openness between *E. cordifolia* recruit types (sprouts and saplings).

	Df	SS	MS	pseudoF	P-value	Explained variance (%)
Recruit type	1	3555	3554.8	34.663	<0.001	6.2
Residuals	523	53637	102.6			93.8
Total	524	57191	1			

Figure 1  
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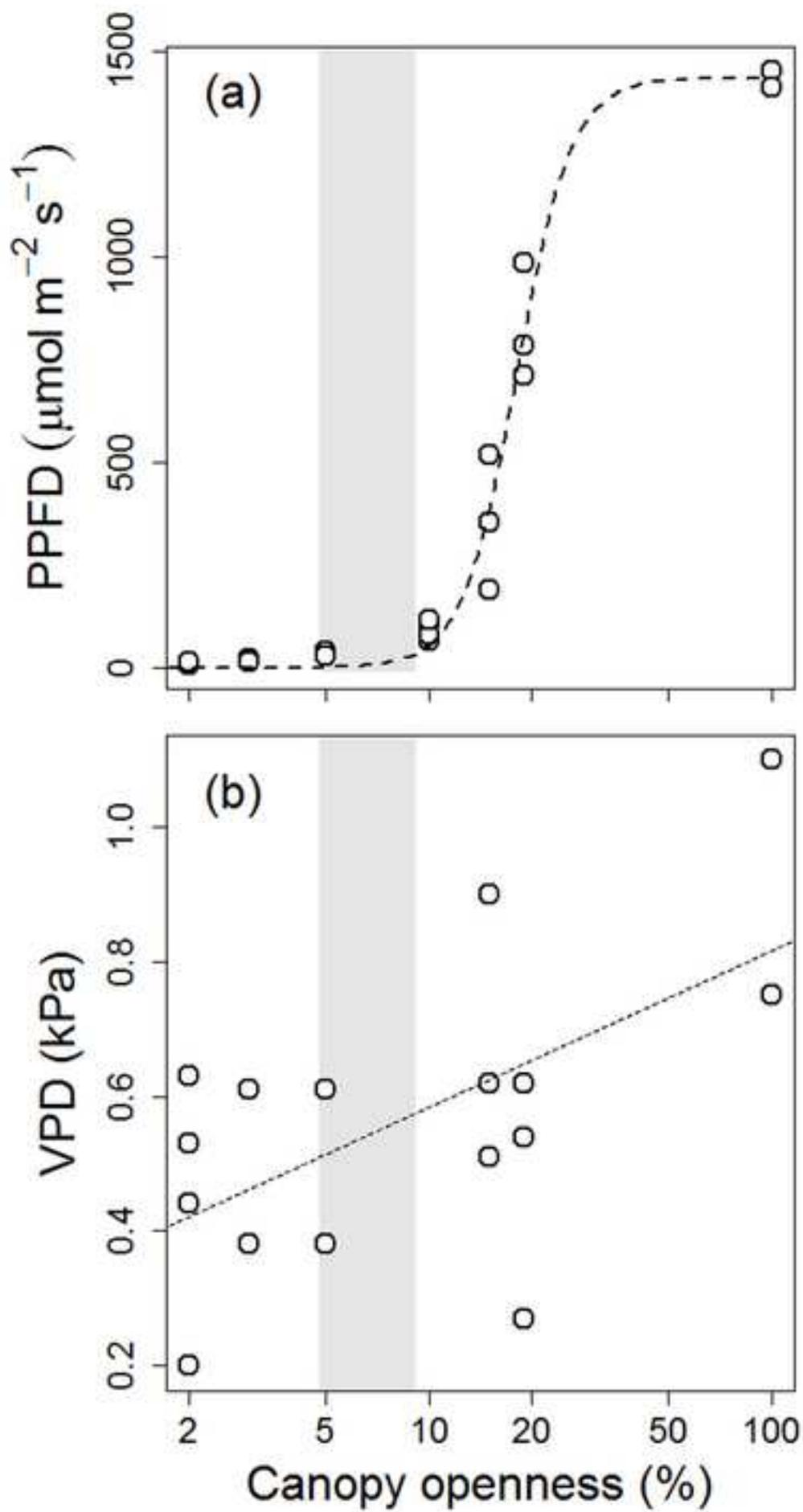


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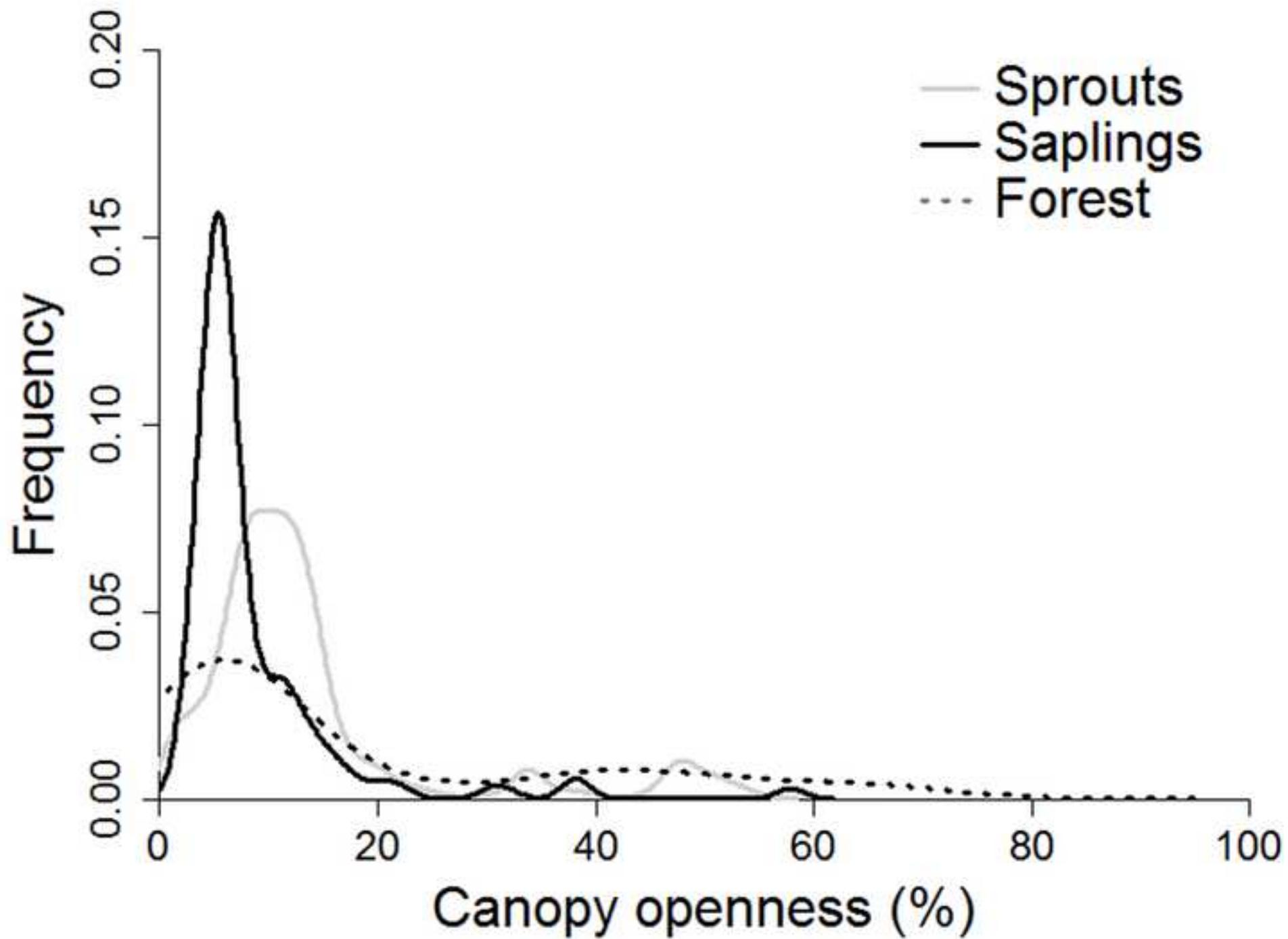
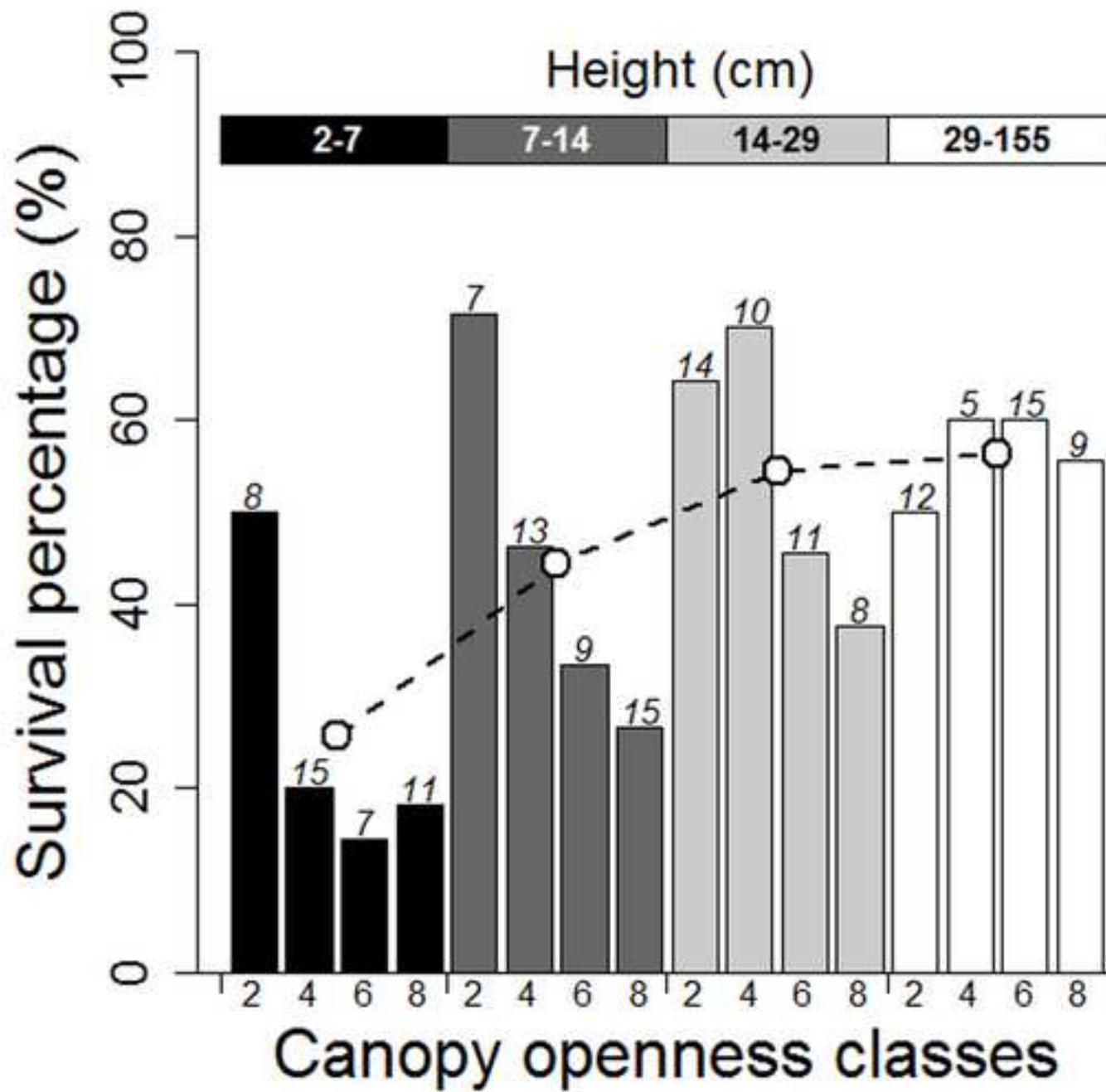


Figure 3  
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