1   # Lack of negative density-dependence regulation in a dominant

2   # oak tree from a neotropical highland forest

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21   **Abstract:** Conspecific negative density-dependence (CNDD) is one of the main mechanisms proposed to

22   regulate species coexistence. Tropical highland forests, in contrast to diverse lowland forests, are

23   commonly dominated by a few tree species. Testing the importance of density-dependence effects on

24   seedling establishment of dominant trees may provide insights on the mechanisms regulating population

25   dynamics and forest composition of tropical highlands. We tested the importance of CNDD regulation on

26   seedling survival and recruitment of *Quercus costaricensi*s, a monodominant oak in the Talamanca

27   highland forests of Costa Rica. We used spatial statistics and generalized linear mixed models to test the

28   effects of conspecific density, distance to the nearest adult, density of *Chusquea* bamboo shoots, and

29   herbivory on the annual survival probability of 3538 seedlings between 2014 and 2017. We did not find

30   any effect of CNDD on seedling survival. However, bamboo density and herbivory both significantly

31   decreased seedling survival. All seedlings had signs of herbivory and predator satiation may explain the

32   lack of density dependent regulation in this species. We argue that the lack of intraspecific density

33   regulation at the seedling stage may explain the dominance of *Q. costaricensis* in the highland forests of

34   Costa Rica. Local density of this endemic oak is instead regulated by herbivory and the density of

35   *Chusquea*.

36   ## Key words:

37   Density-dependence, Janzen-Connell hypothesis, herbivory, masting, seedling recruitment, oak forest

38   ## Introduction

39   Conspecific negative density-dependence (CNDD) reduces seedling survival and recruitment in

40   many tree species when conspecific density is high. This negative effect likely results from antagonistic

41   intra- and interspecific plant interactions, pathogens and herbivores attracted to high-density patches or

42   through infestation from adults (Janzen 1970; Connell 1971; Freckleton and Lewis 2006; Bagchi et al.

43   2010; Fricke et al. 2014). Janzen (1970) and Connell (1971) independently proposed that higher offspring

44   mortality of abundant species reduces competition for other species with similar ecological requirements,

45   but susceptible to different enemies, leading to an increase in species diversity. Since then, there has been

46   great interest in testing the importance of this regulating mechanism in both tropical (Clark and Clark

47   1984; Wright 2002; Peters 2003; Comita et al. 2014) and temperate forests (Hille Ris Lambers et al. 2002;

48   HilleRisLambers and Clark 2003; Yamazaki et al. 2008).

49   Although most ecologists agree on the ubiquity and importance of CNDD regulation in tropical

50   forests (LaManna et al. 2017), susceptibility to conspecific density may vary across species (Comita et al.

51   2010; Lin et al. 2012). Rare species are expected to be less affected by CNDD since their populations are

52   small and may not be able to sustain large predator populations (Connell et al. 1984). However, recent

53   findings show that common species are less likely to be affected by CNDD due to a combination of

54   physiological traits and high additive genetic diversity in genes associated with immune responses

55   (Comita et al. 2010; Marden et al. 2017). In tropical plant species, CNDD regulation commonly occurs at

56   the seedling stage and seed-to-seedling transition. Several traits such as a seedling's shade tolerance or

57   leaf traits (Kobe and Vriesendorp 2011), soil nutrients (LaManna et al. 2016) and diversity and abundance

58   of soil pathogens (Bagchi et al. 2010; Bever et al. 2012), may all influence seedling tolerance to high

59   conspecific densities or to the antagonistic effects of nearby adults (i.e., asymmetric competition).

60   Tropical forests are commonly perceived as highly diverse habitats, however, tropical montane

61   forests (above 2500 m asl) have fewer species compared to lowland tropical forests and are commonly

62   dominated by a few tree species (Connell and Lowman 1989; Richards 1996; Lieberman et al. 1996).

63   Thereby processes structuring these low diversity tropical forests are not yet fully understood (Hart et al.

64   1989). In Costa Rica and western Panamá, montane forests are dominated by oaks (Kappelle 2006).

65   *Quercus costaricensis* Liebm. (Fagaceae) is restricted to the Talamanca mountain range, where it

66   represents over 90% of the basal stem area (stems >50 cm dbh) with several thousand juveniles per

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67   hectare (Kappelle 2006). Although the dynamics of tropical oak communities have been scarcely studied;

68   temperate oaks have been shown to be susceptible to CNDD and distance to the nearest adult (Wada et al.

69   2000). In contrast, ectomycorrhizal transfer from adults to close by seedlings seems to have a positive

70   effect on seedling density and survival (Dickie et al. 2002). Therefore, factors regulating seedling

71   recruitment in oaks could be species or population specific, so that conspecific density could either lower

72   survival through competition and herbivory or increase recruitment by sharing symbionts. Considering

73   the pronounced dominance of *Q. costaricensis* in the highlands of Costa Rica and its large density of

74   seedlings, we expected to find weak (if any) CNDD regulation on seedling survival and we expected to

75   find a positive effect of nearby adults on seedling recruitment.

76   Our main objective in this study was to test for CNDD regulation on survival and recruitment of

77   seedlings of the dominant oak *Q. costaricensis* in the highlands of Costa Rica. Specifically, we tested the

78   effect of conspecific seedling density, distance to nearest adult and herbivory on seedling recruitment and

79   survival. The bamboo *Chusquea* spp. (Poaceae) grows in dense clumps in the understory of montane

80   tropical forests (Widmer 1998) and could be an important factor limiting seedling survival, therefore we

81   also included the effect of bamboo density (*Chusquea* spp.) when studying survival and recruitment of *Q.*

82   *costaricensis* seedlings.

83   **Material and Methods**

84   ***Study area and species***

85   The study was conducted at Cerro de la Muerte Biological Station (CMBS, 09°33' N, 83°44' W;

86   3100–3350 m a.s.l.), in a Costa Rican upper montane tropical forest (Holdridge 1971). The mean annual

87   precipitation is 2500 mm, with a relatively dry period (<200 mm) between January and April, and the

88   mean air temperatures is 12°C, with large daily fluctuations (from –5 ∘C to 35 ∘C) (Fuchs et al. 2010).

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89   The canopy in the study site is dominated by oak trees (*Q. costaricensis*) and the understory by

90   dense clumps of *Chusquea* bamboo (Kappelle et al. 1995; Widmer 1998). *Q. costaricensis* is restricted to

91   upper montane forests (>2200 m elevation) in the Talamanca mountain range in southern Mesoamerica

92   between Costa Rica and Panamá (Hartshorn 1983). Fruiting is synchronous, with a supra-annual masting

93   pattern every two or more years, but flowering occurs every year between December and March

94   (Camacho Calvo and Orozco Vílchez 1998). Acorns fall to the ground between April and October. Seeds

95   germinate after 7 days in controlled conditions, and germination success is 91% (Quirós-Quesada 1990).

96   *Q. costaricensis* hosts both arbuscular- and ecto-mycorrhizal fungi and seedling growth responds

97   positively to these symbionts (Holste et al. 2017). *Quercus* seedlings are highly dependent on cotyledons

98   reserves during early development (Yi et al. 2015) and seed size could have a positive effect in

99   establishment success (Bonfil 1998).

Seedling censuses

101   We set four 400-m^2 plots (20 x 20 m) within CMBS. Plots were placed in old growth forests

102   undisturbed for at least 30 years. Plots were subdivided into 64 (2.5 x 2.5 m) quadrats to ease seedling

103   censuses. The density of *Chusquea* stems varied naturally among plots (0 to 14 stems m^{-2}). On February

104   2014, we mapped and tagged all *Q. costaricensis* seedlings (height < 2m) within each plot. We also

105   mapped and measured DBH (> 5 cm) of all adult trees within the plot and in a 10 m wide buffer area

106   around each plot. For each seedling, we measured its height, distance to the nearest conspecific adult and

107   the conspecific seedling density in a 1m radius around each seedling. We also estimated leaf damage by

108   using the qualitative index of herbivory (IH) developed by Núñez-Farfán and Dirzo (1988). For each

109   quadrat, we also counted the number of bamboo stems.

110   On May/June 2015, 2016 and 2017; we re-censused all plots and determined annual seedling

111   mortality and recruitment per quadrat. A seedling was considered dead when its stem was dry and

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112   leafless, rotten or when missing in two consecutive censuses. Dead individuals were removed from

113   survival analyses for the following years. This oak population produced fruits in 2014 and 2016, but less

114   than 15% of adults reproduced in 2016, therefore we considered the 2014 fruiting year as the only

115   masting event during the study period. In 2014, censuses were conducted before acorns had fallen, to

116   avoid including newly germinated seedlings. In 2015, new untagged seedlings were included as the 2015

117   cohort from the 2014 masting event. These new recruits were easily identified because cotyledons were

118   attached to most seedlings, even after one year. Recruits were mapped and their height and herbivory

119   indexes were also recorded, except in those cases in which seedling leaves were not fully developed (ca.

120   1% or 15 seedlings). New recruits were included on survival analyses for the following years. Acorns

121   were not produced in 2015 therefore on the 2016 census we only recorded seedling mortality. The few

122   recruits we tallied in 2016 (55 in total) were taller than expected for new seedlings, so they were probably

123   uncounted seedlings from the previous census, thus we considered them as 2015 recruits. Only a few

124   adults reproduced in 2016 (not a masting year), thus we only recorded five new seedlings in 2017 on all

125   four plots; therefore we only analyzed recruitment success after the 2014 masting.

126   ***Spatial analyses***

127   Both the CNDD regulation and the Janzen-Connell effect depend on seed dispersal and its

128   resulting spatial aggregation. It assumes that seedlings are spatially aggregated. We analyzed the spatial

129   distribution of seedlings in our plots using the $L(t)=(K(t)/\pi)^{0.5}$ transformation of the univariate Ripley's

130   *K*(*t*) function (Ripley 1977), for the 2014 seedlings. We used the R statistical language (Version 3. 2. 2;

131   Core Team 2016) for all spatial analyses (''spatstat'' library, Baddeley et al. 2016).

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132   ***Survival and recruitment analyses***

133   We modeled the annual probability of seedling survival for three years between 2014 and 2017, as a

134   function of initial height, intraspecific seedling density, distance to nearest conspecific adult tree,

135   herbivory, and *Chusquea* density using a generalized linear mixed-effects model with a *binomial*

136   distribution (Bolker et al. 2009). All variables, as well as the log-transformed seedling height, were

137   standardized and entered in the model as fixed effects. Quadrat and census year were included as random

138   effects. We also included a dummy variable (age) as a fixed factor that identified seedlings from the 2014

139   census and those recruited in 2015 to determine if newly recruited seedlings had a different survival

140   probability. A second-degree polynomial effect for distance to nearest adult conspecific was also tested. A

141   full model was built including all variables and all second order interactions. To test Janzen-Connell

142   predictions, we analyzed the effect of seedling density and distance to the nearest adult on seedling

143   herbivory (IH). We retain models that included all the variables of interest, significant interactions, and

144   significant polynomial terms (Table S1).

145   We also analyzed seedling recruitment per quadrat to account for spatial variation in recruitment

146   within a plot. This analysis included only the 2015 data, one year after the masting event of 2014. We

147   used a GLMM with a *quasi-poisson* distribution to estimate the effect of seedling density (number of

148   seedlings per quadrat), conspecific tree density (number of tree trunks in a 2.5 m radius around the center

149   of the quadrat) and *Chusquea* density on seedling recruitment. All explanatory variables were

150   standardized to facilitate comparisons between effects. Plots were included as a random effect to account

151   for spatial autocorrelation of seedlings located within the same plot (Lin et al. 2014). We used the *lme4*

152   package (Bates et al. 2015) in R language (Version 3. 2. 2; R Core Team 2016) for statistical analyses.

Results

In the 2014 census we mapped and tagged 2031 seedlings, which were spatially aggregated at all scales (Fig. S1). Herbivory was common; over 99% of censused seedlings had some leaf damage and most plants (ca. 71%) had intermediate damage (10-75%), as recorded by the Index of Herbivory (Fig. 1). Contrary to expectations of the Janzen-Connel hypothesis, herbivory decreased at higher seedling densities and increased away from adults (Table S2).

Annual seedling survival decreased slightly over the study period, from 73.2% in 2015 to 64.38% (2016) and 63.8% (2017). Seedling height had the strongest positive effect on seedling survival, while bamboo density and herbivory (IH) both reduced survival (Fig. 2). The effect of near adults on seedling survival was best described by a negative polynomial function; seedling survival was highest at intermediate distances from adults (Fig. 2). We found a significant interaction between seedling and *Chusquea* densities: high seedling density significantly increased seedling survival at low bamboo densities (<2.4 stems per m^2), and decreased survival at higher bamboo densities (Fig. S2). There were no significant interactions between seedling density and herbivory, nor between herbivory and the distance to the nearest adult (Table S1).

In 2015 we recorded 1578 new recruits. Herbivory was on average lower in new recruits (22.9% leaf damage $\pm$ 1.06) compared to seedlings from the 2014 census (43.75% leaf damage $\pm$ 0.91; t = 25.798, df = 2828.2, p< 0.0001; Fig.1). Seedling recruitment significantly increased with conspecific seedling density, but the number of new recruits failed to correlate with adult density or with *Chusquea* density (Table S1). Interactions between main factors (seedling, *Chusquea* and tree density) had no effect on seedling recruitment.

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Discussion

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175   Seedlings of the endemic oak species, *Q. costaricensis*, occurred in high density and were

176   spatially aggregated as expected for a masting species with gravity-dispersed seeds (Pulido 2002; Hou et

177   al. 2004). Seedling survival exceeded 63% per year, indicating a relatively high success of seedlings

178   during early recruitment and capacity to survive in dense aggregations. In spite of the densely aggregated

179   distribution of seedlings, we did not detect significant CNDD regulation on seedling survival or

180   recruitment. A similar situation has been reported for other lowland tropical tree species with masting

181   reproduction. For example, several Dipterocarps (Dipterocarpaceae) in Asia (Delissio et al. 2002) or the

182   legume *Dicymbe corymbosa* (Fabaceae) in South America and *Gilbertiodendron dewevrei* in Africa (Hart

183   1995; Henkel 2003; Henkel et al. 2005); all produce copious amounts of seeds and dense seedling

184   aggregations that escape the negative effects of CNDD regulation; resulting in high adult densities. The

185   lack of negative effects of conspecific density on seedlings establishment of *Q. costaricensis* could

186   contribute to its dominance in Costa Rican montane forests.

187   Herbivory significantly increased seedling mortality. Loss of leaf area and possible invasion of

188   pathogens through damaged tissue are expected to increase mortality and lower the competitive ability of

189   seedlings (Frost and Rydin 1997). Despite herbivory being ubiquitous in seedlings, survival after three

190   years was high (over 62%) and was unrelated to conspecific density or distance to the nearest adult. These

191   findings disagree with expectations posed by the Janzen-Connell negative density regulation, in contrast,

192   we found a positive effect of density on seedling survival. One possible explanation for the relatively high

193   survivorship of seedlings that we observed, given the high density of oak seedlings (2.4 seedlings m^{-2}),

194   could be herbivore satiation (Janzen 1974; Visser et al. 2011; Bagchi et al. 2011). If herbivore satiation

195   occurs, its effect on survival or recruitment is expected to decrease at higher seedling density, when a

196   larger amount of edible tissue is available. Our results support this hypothesis as we recorded higher

197   seedling survival after the masting event (2014-2015, 73.2%) when seedling number increased. We also

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198 found a positive effect of density on seedling recruitment. Seeds were more likely to germinate in areas of

199 higher seedling density, where they escape both seed predation and herbivory.

200 Variability in the relative strength of CNDD regulation between common and rare species has

201 been proposed to have a main effect on determining tree diversity and species composition (Hubbell et al.

202 2001; Comita et al. 2010). Fricke and Wright (2017) argue that in tropical forests, dominant tree species

203 are expected to have weaker CNDD . The apparent lack of CNDD regulation in *Q. costaricensis*

204 correlates with its high abundance in montane forests and may result from different interacting life history

205 traits (Comita et al. 2010; Zhu et al. 2018). For instance, Kobe and Vriesendorp (2011) found that

206 seedlings from shade tolerant species were less affected by CNDD in lowland tropical forests and

207 suggested that they had better defenses and responses to herbivores. A similar result was found by Zhu et

208 al. (2018) for slow growing tropical species. Abundant species also tend to have low levels of foliar

209 damage that increases individual's survivorship (Torti et al. 2001). Most seedlings showed low to

210 intermediate levels of herbivory, which does not contribute significantly to CNDD regulation in this

211 Costa Rican oak. High tolerance to leaf damage or long-lived leaves which accumulate minor damage

212 over time, may better explain the observed levels of seedling herbivory.

213 Ectomycorrizal (ECM) associations increase nutrient acquisition in oak species (Smith et al.

214 1997), and this may provide an additional advantage to seedling establishment of *Q. costaricensis* . Many

215 dominant tropical trees are associated with ectomycorrhizae and this symbiosis often contributes to their

216 abundance (McGuire et al. 2008). McGuire (2007) found that seedlings from the monodominant tropical

217 tree *D. corymbosa* have a positive input from the ECM network, reducing CNDD effects and increasing

218 seedling survival near parental trees. A balance between asymmetric competition and indirect facilitation

219 by ectomycorrhizal transfer from adults to seedlings increase their survival at intermediate adult densities

220 in *Quercus rubra* (Dickie et al. 2002). Our results show that seedling survival has a negative quadratic

221 relationship with distance to the nearest adult; suggesting that at intermediate distances seedling survival

222   is higher probably due to ECM transfer from adults. At greater distance, ECM colonization may decrease,

223   and competition and CNDD may interact to reduce seedling survival. Given the high density of seedlings

224   near adults, the potential transfer of ECM from adult *Q. costaricensis* may allow seedlings to escape the

225   negative effects of CNDD or mortality through the different mechanisms proposed by Janzen-Connell

226   (Holste et al. 2017).

227   ### *The role of interspecific interactions regulating oak population*

228   Interspecific plant interactions play an important role in oak seedling recruitment and survival.

229   The observed aggregated distribution of oak seedlings may be partly determined by localized seed

230   dispersal, but also by differential recruitment influenced by the occurrence of dense patches of *Chusquea*

231   bamboo. The dense thickets formed by bamboo stems strongly reduce oak seedling survival, as they

232   dominate the herbaceous layer limiting the establishment and growth of tree seedlings due to resource

233   competition reducing space available for colonization (Veblen et al. 1979; Royo and Carson 2006; Itô and

234   Hino 2007). The density of bamboo shoots may also significantly increase oak seedling mortality through

235   different mechanisms: resource competition, allelopathy, and physical interference (Veblen 1982; Esteso-

236   Martínez et al. 2006; Royo and Carson 2006). Though *Q. costaricensis* seedlings are shade tolerant

237   (Camacho and Bellefleur 1996), the extreme dense layer of bamboo plants that cover oak seedlings

238   largely reduce the amount of photosynthetic active radiation that reaches the understory, hindering the

239   photosynthetic activity of oak seedlings, and reducing water availability during low precipitation months,

240   since bamboo water intake is very high (Esteso-Martínez et al. 2006). Bamboo could also indirectly

241   interfere with oak seedling development by modifying soil composition; *Chusquea* spp. change the

242   concentration of soil nutrients and litter thickness which may inhibit seedlings establishment or

243   development as observed for *Nothofagus* spp. (Nothofagaceae) in South America (Veblen 1982).

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244   *Chusquea* spp. can also hinder the growth of ECM fungi or interfere with their root associations

245   increasing seedling mortality (Wolfe et al. 2008).

246   In conclusion, the high density of this endemic oak tree in the Costa Rican montane forests is

247   likely the result of predator satiation and adult facilitation through ectomycorrhyzal transference from

248   nearby conspecifics, which results in an apparent absence of CNDD regulation on seedling survival and

249   establishment. Herbivory and interspecific competition with *Chusquea* bamboo appear to be important

250   factors controlling seedling density of this species; but neither of them were density dependent. This lack

251   of CNDD regulation concurs with expectations for dominant tropical trees (Comita et al. 2010).

252   Environmental factors may also influence the strength of CNDD regulation. For example, LaManna et al.

253   (2016) found that the strength of CNDD increases in resource-rich environments. Harsh conditions in

254   montane forests (e.g., acidic soils, low temperatures, high solar irradiance; Kappelle 1996) could impact

255   plant community composition and abundance of natural enemies (McCain and Grytnes 2010), which in

256   turn may alter CNDD regulation (Mangan et al. 2010). However, these factors were beyond the scope of

257   this study.

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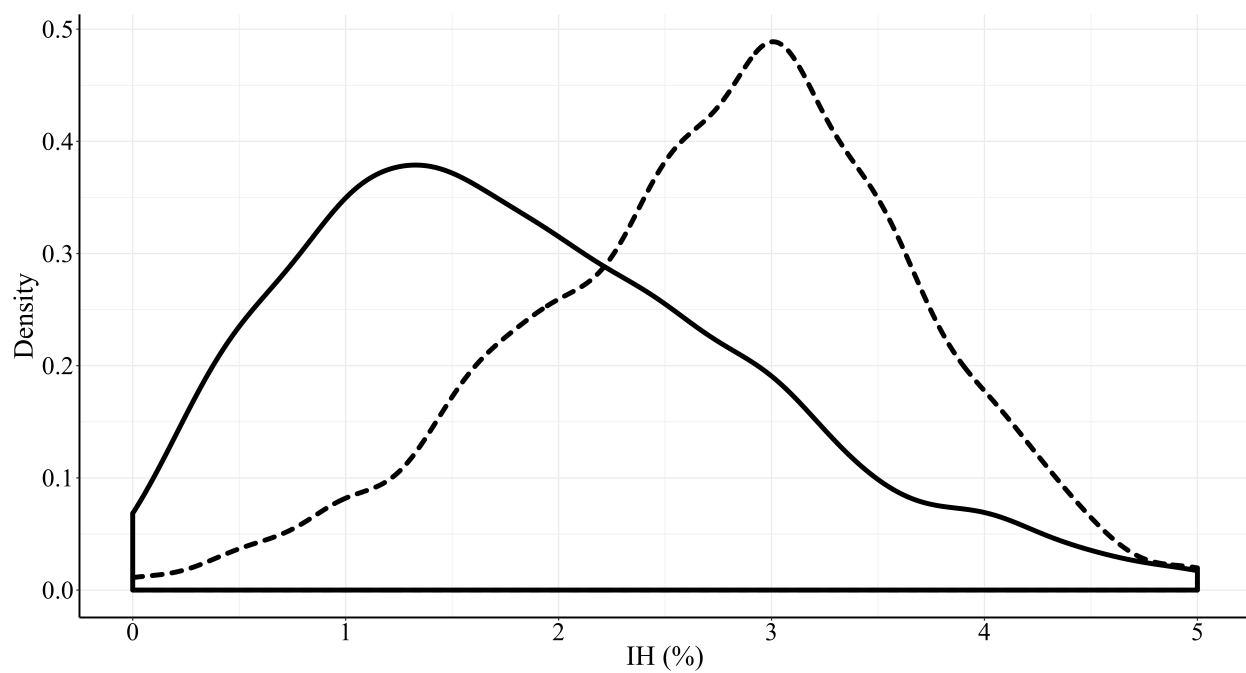
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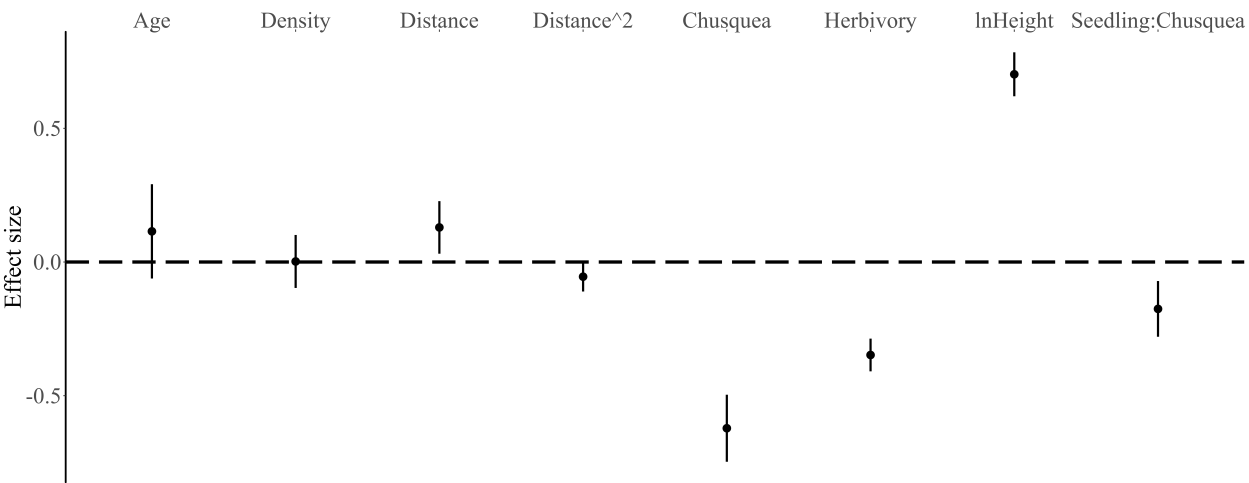
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444 **Figure captions**

445 **Fig. 1** Density distribution of the herbivory index (IH) for seedlings of *Quercus costaricensis* (Fagaceae)

446 in a tropical montane forest in Costa Rica. Dashed line represents seedlings established before the masting

447 event of 2014 (N=2031) and solid line, 2015 recruits (N=1578)

448

449 **Fig. 2** Estimated standardized GLMM effects (±1.96 SE) of factors affecting seedling survival in *Quercus*

450 *costaricensis* from 2014 to 2017 in a tropical montane forest in Costa Rica. *Age:* describes whether

451 seedlings were censused in 2014 or in 2015; *Density*: intraspecific density within a 1m radius; *Chusquea*:

452 density of bamboo stems; *Distance:* distance to the nearest conspecific adult; *Herbivory:* Herbivory

453 index; *lnHeight:* logarithm of seedling height; *Seedling: Chusquea:* interaction between seedling density

454 and *Chusquea* density

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