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How does habitat filtering affect the detection of conspecific and phylogenetic density dependence?

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1   Running Head: **Habitat filtering and density dependence**

2

3   **How does habitat filtering affect the detection of conspecific and phylogenetic density**

4   **dependence?**

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14

15   **Abstract**

16   Conspecific negative density-dependence (CNDD) has been recognized as a key mechanism

17   underlying species coexistence, especially in tropical forests. Recently, some studies have

18   reported that seedling survival is also negatively correlated with the phylogenetic relatedness

19   between neighbors and focal individuals - termed phylogenetic negative density-dependence

20   (PNDD). In contrast to CNDD or PNDD, shared habitat requirements between closely related

21   individuals are thought to be a cause of observed positive effects of closely related neighbors,

22   which may affect the strength and detectability of CNDD or PNDD. In order to investigate the

23   relative importance of these mechanisms for tropical tree seedling survival, we used generalized

24   linear mixed models to analyze how the survival of more than 10,000 seedlings of woody plant

25   species related to neighborhood and habitat variables in a tropical rainforest in southwest China.

26   By comparing models with and without habitat variables, we tested how habitat filtering affected

27   the detection of CNDD and PNDD. The best-fitting model suggested that CNDD and habitat

28   filtering played key roles in seedling survival, but that, contrary to our expectations, phylogenetic

29   positive density-dependence (PPDD) had a distinct and important effect. While habitat filtering

30   affected the detection of CNDD by decreasing its apparent strength, it did not explain the

31   positive effects of closely-related neighbors. Our results demonstrate that a failure to control for

32   habitat variables and phylogenetic relationships may obscure the importance of conspecific and

33   heterospecific neighbor densities for seedling survival.

34

35

36   **Key words:** *competition, habitat association, Janzen-Connell hypothesis, mixed models,*

37   *phylogenetic relatedness, tropical forest*

38

39

INTRODUCTION

40

41 Tree populations are often thought to be regulated by negative density dependence (NDD),

42 thereby making NDD an important mechanism underlying the maintenance of species diversity

43 across multiple life stages (e.g., Wills et al. 1997, Harms et al. 2000, Peters 2003, Volkov et al.

44 2005, Comita et al. 2010, Swamy et al. 2011, Johnson et al. 2012, Comita et al. 2014).

45 Intraspecific competition and Janzen-Connell effects (Janzen 1970; Connell 1971) via species-

46 specific natural enemies (seed predators, pathogens and herbivores) are two main drivers of

47 NDD (Wright 2002). Many studies have tried to demonstrate NDD by examining the relationship

48 between plant survival, recruitment or growth and the densities of conspecific neighbors. Such

49 studies, typically conducted using seedlings, have frequently found conspecific negative density

50 dependence (CNDD) in the species studied (e.g., Webb and Peart 1999, Comita et al. 2010, Chen

51 et al. 2010, Lin et al. 2012, Johnson et al. 2012).

52   The effects of intra- and inter-specific density on seedlings may be interchangeable if

53 pathogens have wide host ranges where neighborhood density *per se* drives NDD and it is not

54 necessary to invoke CNDD (Freckleton and Lewis 2006). However, tropical forest investigations

55 that have partitioned their analyses into conspecific and heterospecific effects have often found

56 significant differences in intra- and inter-specific effects (e.g., Peters 2003, Comita and Hubbell

57 2009, Johnson et al. 2012, Lin et al. 2012). This has supported the widespread view that seedling

58 performance is limited more by interactions with conspecific individuals than heterospecific

59 individuals. If generally valid, the greater strength of negative intra-specific effects relative to

60 negative inter-specific effects (i.e., niche differences) promotes stable species coexistence

61 (Chesson 2000).

62   Interestingly, conspecific adult neighbor densities have been found to have a particularly

63   strong negative influence on seedling survival (e.g., Comita and Hubbell 2009, Chen et al. 2010,

64   Johnson et al. 2014). Seedling-seedling interactions, in contrast, are often relatively weak,

65   presumably because the sizes and densities of seedlings in the understory of tropical forests are

66   not typically great enough to generate such large impacts (Paine et al. 2008, Svenning et al.

67   2008). Further, positive correlations between the probability of seedling survival and

68   heterospecific neighbor densities have been found (Comita and Hubbell 2009), supporting the

69   so-called 'species herd protection hypothesis' (Peters 2003). Thus, seedling survival is likely to

70   be lower in an area of high conspecific adult neighbor density and higher in an area with many

71   heterospecific adult neighbors.

72   Due to the enormous diversity in the tropics, heterospecific neighbors are more common

73   than conspecific neighbors. A simple division of neighbors into conspecifics and heterospecifics

74   may therefore hide the potentially large variation in the degree to which heterospecific species

75   are similar to the focal species. Such thinking led Webb et al. (2006) to characterize

76   heterospecific species in terms of their phylogenetic distance from the focal individual, thereby

77   moving neighborhood analyses beyond a potentially overly-simplistic conspecific/heterospecific

78   dichotomy.

79   The rationale for considering phylogenetic relatedness in studies of NDD rests on empirical

80   evidence suggesting that there is often a phylogenetic signal in morphological and biochemical

81   traits that dictate host-pest interactions (Mitter et al. 1991). In the most extensive syntheses to

82   date, the probability of sharing a pest or pathogen between two host plants decays strongly with

83   phylogenetic distance (Parker and Gilbert 2004, Novotny et al. 2006, Gilbert and Webb 2007,

84   Gilbert et al. 2012). This pattern is expected to be more pronounced under broader taxonomic

85   samples, and less pronounced under smaller taxonomic samples (e.g., a single genus).

86 Phylogenetic negative density dependence, due to shared natural enemies between closely related

87 species, may therefore be expected to emerge in a tropical forest containing many plant lineages

88 (i.e., a broad taxonomic sample). In such cases, CNDD can be extended across evolutionary

89 distance between two neighboring species (e.g., Webb et al. 2006, Metz et al. 2010, Liu et al.

90 2012, Paine et al. 2012, Lebrija-Trejos et al. 2014) therefore generating phylogenetic negative

91 density dependence (PNDD).

92   Beyond biotic interactions, an important driver of local community composition is the

93 abiotic environment (Metz et al. 2010). For example, variation in light availability (Comita et al.

94 2009, Queenborough et al. 2009, Rüger et al. 2009), soil water availability (Comita and

95 Engelbrecht 2009, Lin et al. 2012) and soil nutrients (Bai et al. 2012) are all well-known drivers

96 of species survival, coexistence and diversity.

97   Findings that survival probability is positively correlated with conspecific density are often

98 interpreted as being due to species' habitat preferences (e.g., Comita et al. 2009, Comita and

99 Hubbell 2009, Lin et al. 2012). Indeed, many studies examine species' habitat preferences by

100 analyzing the association between species occurrence and habitat variables (e.g., topography,

101 light, soil nutrients, water availability etc.) at the seedling stage (e.g., Webb and Peart 2000, John

102 et al. 2007, Comita et al. 2007, Comita and Engelbrecht 2009, Metz 2012). However, we argue

103 that such results do not necessarily indicate a lack of biotic interactions in general or NDD in

104 particular. Specifically, biotic interactions are dictated by the abiotic context, and a shared habitat

105 preference does not negate the possibility of NDD. Rather, it is likely that habitat preferences and

106 NDD operate simultaneously to produce observed species composition and population dynamics

107 (e.g., Comita et al. 2009, Chen et al. 2010, Bai et al. 2012, Piao et al. 2013). In order to elucidate

108 such a scenario, nested models that consider density effects without and with the abiotic context

109   are needed.

110   In this study, we used a population dynamics dataset of 10,316 seedlings for 269 woody

111   plant species for four contiguous one-year census intervals in the 20-ha Xishuangbanna tropical

112   seasonal rainforest dynamics plot in southwest China. Using generalized linear mixed models,

113   we explored the relative importance of CNDD, PNDD and habitat filtering for seedling survival.

114   Specifically, we built models of seedling survival dependent on the densities of conspecific and

115   heterospecific neighbors and on the phylogenetic dissimilarities between heterospecific

116   neighbors and focal seedlings. Each of these models was built without and with habitat variables

117   to determine the degree to which habitat filtering affected the apparent prevalence of NDD. We

118   specifically ask: (*i*) Does scaling the effects of neighbors by their phylogenetic distances improve

119   model fit?; (*ii*) What is the relative importance of CNDD, PNDD and habitat filtering in our

120   study system?; and (*iii*) How does habitat filtering affect the detectability of CNDD and PNDD?

121

122   **METHODS**

123   Study site

124   The study was conducted within the 20-ha Xishuangbanna Forest Dynamics Plot (XSBN),

125   located in Mengla, Yunnan Province, Southwestern China (101°34′ E, 21°36′ N). The elevational

126   range of the plot is from 709 m above sea level (asl) to 869 m asl (Lan et al. 2012) (Fig. S1).

127   There is a rainy season from May to October and a dry season from November to April in the

128   following year. Mean annual precipitation is approximately 1500 mm, of which 80% occurs from

129   May to October (Cao et al. 2006).

130   The XSBN plot (400×500 m) was established in 2007 and censuses are carried out every 5

131   years. All woody stems with a diameter at breast height (DBH) ≥ 1 cm are tagged, identified,

132   measured and mapped (See detailed methods in Condit 1998). A detailed description of the

133   climate, geology and flora of XSBN can be found in Cao et al. (2008).

134

135   Seedling quadrats

136   During March 2010, a total of 500 seedling quadrats (2×2 m) were established in a regular

137   pattern in the center of each 20×20 m subplot in the 20-ha XSBN plot. Where obstacles such as

138   streams, large trees, rocks or fallen woods prevented the establishment of seedling quadrats in

139   these locations, they were placed instead in nearby 5 × 5 m subplots. In each of the 500 seedling

140   quadrats, all woody (tree, shrub and liana) seedlings with DBH < 1 cm and height ≥ 20 cm were

141   tagged, identified to species and measured for height. In this study, we used seedlings with height

142   ≥ 20 cm as focal seedlings because seedlings with this height can be assumed to be established in

143   our study system, and therefore more likely to be dependent upon relevant biotic and abiotic

144   interactions rather than effects of chance events that drive mortality in younger seedlings.

145   Seedling quadrats were subsequently censused in the late dry season (April and May) 2010,

146   2011, 2012, 2013 and 2014. In each census, the states (alive or dead) of all the woody seedlings

147   alive at the previous census were recorded and all new recruits to the 20-cm height threshold

148   were identified and tagged.

149

150   Neighborhood variables

151   At the first (2010) census, we defined total seedling neighbor density of each seedling quadrat as

152   the number of seedlings within the quadrat. Conspecific and heterospecific seedling neighbor

153   densities were defined in the same way. At subsequent censuses, we recalculated seedling

154   neighbor densities by excluding dead seedlings and adding newly recruited seedlings. Tree, shrub

155   and liana seedlings were monitored at the censuses, and all were included in the calculation of

156   heterospecific seedling neighbor densities, although lianas were not included as focal seedlings

157   in our models. Seedlings that were impossible to classify by species (121 in the 2010 census)

158   were included in heterospecific neighbor counts, but not as focal seedlings.

159   We calculated the total adult neighbor density (TA) as the summed basal area (BA) of

160   nearby adults weighted by their distances to the focal seedling (Canham et al. 2004):

161
$$TA = \sum_i^N \frac{BA_i}{Distance_i}$$

162   where N is the number of adult neighbors. Conspecific and heterospecific adult neighbor

163   densities were calculated in the same way. Models with densities calculated over a distance of 20

164   m had stronger support than those with densities calculated over distances of 10 m or 30 m

165   (Table S1). In the following analyses, we therefore used total, conspecific and heterospecific

166   adult neighbor densities calculated over 20 m. As a result, data from 86 of the 500 seedling

167   quadrats were excluded from the following analyses because these quadrats were within 20 m of

168   the edge of the XSBN plot, and therefore had incomplete adult neighbor density values.

169

170   Construction of phylogenetic tree and indices of phylogenetic dissimilarity

171   We have previously produced a molecular phylogeny for 428 species in the 20-ha XSBN plot

172   (Yang et al. 2014). A total of 121 species identified in the 20-ha plot and/or the seedling quadrats

173   were added to this phylogeny using the APE package (Paradis 2006) in R software (v. 3.0.2) (R

174   Development Core Team 2014). These species were added at the crown node of the most closely

175   related taxonomic level (genus, family or order) in the original molecular phylogeny. For

176   example, any species missing from the original phylogeny that had a congener in the original

177   phylogeny was manually added to the phylogeny at the node for that genus. If there was no

178   congener in the original phylogeny, then the species was added to the node for its family in the

179   original phylogeny. A total of 18 species could not be added to the phylogeny because they were

180   from orders not in the original phylogeny. These species only constituted < 1 % of all individuals

181   in the seedling quadrats and therefore had little influence on our results.

182   Four phylogenetic diversity indices quantifying phylogenetic dissimilarity between focal

183   seedlings and their heterospecific neighbors were used in our analyses: total phylogenetic

184   diversity (TOTPd), average phylogenetic diversity (AVEPd), relative average phylogenetic

185   diversity (APd') and relative nearest taxon phylogenetic diversity (NTPd'). The TOTPd and

186   AVEPd are, respectively, the sum and average of the phylogenetic distances between a focal

187   seedling and its heterospecific neighbors. The APd' and NTPd' (proposed by Webb et al. 2006)

188   respectively quantify the deviation of observed average phylogenetic distance between a focal

189   seedling and its heterospecific neighbors from that expected under a null model, and the

190   equivalent deviation of observed phylogenetic distance between a focal seedling and its most

191   closely-related   heterospecific neighbor. The null model used in this study shuffled the names of

192   species on the phylogeny 999 times to produce a null distribution of neighborhood phylogenetic

193   diversities. Positive APd' and NTPd' indicate that neighbors are less related to the focal seedling

194   than expected under the null model and negative APd' and NTPd' indicate that the neighbors are

195   more related than expected. We recalculated the four phylogenetic diversity indices at each

196   census after 2010 to exclude dead seedlings and add newly recruited seedlings. The indices were

197   calculated separately for heterospecific seedling neighbors and heterospecific adult neighbors

198   (with the adult neighborhood again defined as having a radius of 20 m).

199

200   Habitat variables

201   Habitat variables for each of the 414 target seedling quadrats were characterized using

202   measurements of canopy openness, soil properties and topography.

203   *Canopy openness:* For each seedling quadrat, hemispherical photographs were used to

204   obtain a measure of canopy openness (Comita et al. 2009, Queenborough et al. 2009), which

205   indicated the light condition in the understory. Hemispherical photographs was taken 1.3 m

206   above-ground at the center of each quadrat, using a Nikon Coolpix 4500 camera equipped with a

207   Nikon FC-E8 Fisheye Converter lens in January 2014. The camera was arranged horizontally

208   with the aid of a spirit level and pointed to the geographic south. Black and white JPG-images of

209   2272×1704 pixels were produced in accordance with the methods of Queenborough et al. (2009).

210   The 'high contrast' setting increased distinction between sky and foliage. Three to five replicate

211   photos were taken using a fixed aperture of f/7.5 and shutter speeds between 1/1000 and 1/30 s.

212   Photographs were taken in uniformly overcast weather, during either early dawn or late dusk.

213   The photograph showing the highest contrast between sky and foliage for each quadrat was

214   selected. Gap Light Analyser software (GLA, version 2.0) was used to convert photographs to a

215   single canopy openness measure following the protocol of Beaudet and Messier (2002).

216   *Soil properties:* Soils were sampled following the protocol of John et al. (2007). The 20-ha

217   plot was divided into regular grid squares of 30×30 m, and two soil samples were taken at depths

218   of 10 cm (without litter and humus) and random distance combinations of 2 m and 5 m, 2 m and

219   15 m, or 5 m and 15 m in a random direction from the grid point. A total of 765 soil samples

220   were obtained. Soil pH, organic matter content (C), total nitrogen (TN), total phosphorus (TP),

221   total potassium (TK), available nitrogen (AN), available phosphorus (AP), available potassium

222   (AK) and soil bulk density within each sample were measured (for details see Hu et al. 2012).

223   We used the residuals from polynomial trend-surface regressions for these soil variables to

224   compute empirical variograms, to which we fitted variogram models and used ordinary kriging

225   to obtain spatial predictions of soil variables for each seedling quadrat. This kriging interpolation

226   was implemented using the gstat package (Pebesma 2004) in R software (v. 3.0.2) (R

227   Development Core Team 2014). The volumetric soil water content (%) was measured in the late

228   dry season of 2013, using the mean values of three replicates taken randomly around the center

229   of each seedling quadrat using a TDR probe (MPM-160B) at a depth of 5 cm (Song et al. 2013).

230   *Topography:* The topographic variables used were elevation, convexity, slope and aspect for

231   each seedling quadrat. As above, the full plot was divided into 500 20×20 m subplots with

232   seedling quadrats located at the centers of these subplots. The elevation of each seedling quadrat

233   was taken as the mean of values at each of the four corners of the 20×20 m subplots. The

234   convexity of each seedling quadrat was calculated by subtracting the mean of the four corner

235   elevations of the surrounding 20×20 m subplots from the elevation at its center. The slope was

236   calculated as the mean angular deviation from horizontal of each of the four triangular planes of

237   the 20×20 m subplot formed by connecting three of its corners. Aspect was calculated as below:

238
$$\text{Aspect}=180-\arctan\left(\frac{fy}{fx}\right)\times\left(\frac{180}{\pi}\right)+90\times(\frac{fy}{|fx|})$$

239   Where fx was the elevation difference from east to west in the 20×20 m subplot while fy was that

240   from North to South.

241   To reduce the colinearity of habitat variables in our models, we used a principal components

242   analysis (PCA) in the Vegan package (Dixon 2003) of the R software (v. 3.0.2) (R Development

243   Core Team 2014) on the fourteen habitat variables (soil pH, C, TN, TP, TK, AN, AP, AK, soil

244   bulk density, soil moisture, elevation, slope, aspect and convexity). Canopy openness was not

245   included in the PCA and was inserted into models directly. The first two principal components,

246   accounting for 56.96% variation of these fourteen habitat variables, were used in the later

247   analysis. The first principal component was associated with high elevation and convexity, and

248   low TN, TP, TK, AN, AP, AK, C, pH and soil moisture. The second principal component was

249   associated with high TN, AN, C, elevation and convexity, and low AK, pH, soil bulk density and

250   soil moisture (Table S2).

251

252   Statistical analysis

253   We conducted analyses separately for all living seedlings in each census interval (2010-2011,

254   2011-2012, 2012-2013 and 2013-2014). Living seedlings at any one census included survivors

255   from the previous census and new recruits from the most recent census interval.

256   Generalized linear mixed models (GLMMs) were constructed using the lme4 package (Bates

257   et al. 2014) in R software (v. 3.0.2) (R Development Core Team 2014) to model the probability

258   of seedling survival as a function of explanatory variables, with binomial errors (Bolker et al.

259   2009). Due to the unknown age of seedlings in this study, we included seedling height as a

260   covariate in our models to account for the fact that larger seedlings have higher survival, and

261   therefore to approximately exclude effects of age on survival. The focal seedling height was log-

262   transformed, and all continuous explanatory variables were standardized by subtracting the mean

263   value of the variable (across all individuals in the analysis) and dividing by 1 standard deviation

264   before analyses. This allowed us to compare directly the relative importance of these explanatory

265   variables (Gelman and Hill 2006). The means and ranges of all continuous explanatory variables

266   used in the analysis are listed in Table S3.

267   It is possible that spatial autocorrelation exists in seedling survival due to unexplored

268   habitat and other factors. However, previous studies have found that spatial autocorrelation in

269   tropical seedling survival is negligible at distances >5 m (Queenborough et al. 2007), and

270   seedling quadrats in this study were spaced 20 m apart. Therefore, we added random 'seedling

271   quadrat' effects to our models to exclude any effect of spatial autocorrelation within quadrats on

272   our results. Previous studies suggest that this should be sufficient to account for autocorrelation

273   (Comita et al. 2009, Chen et al. 2010). Furthermore, we included species identity as a random

274   effect, because seedlings of different species were expected to respond differently to local

275   neighborhood variables (Lin et al. 2012).

276   In the simplest, density-independent model, seedling survival depended only on the initial

277   heights of focal seedlings (Table 1, Appendix 1). This model was grounded in evidence that the

278   probability of seedling survival increases with increasing seedling stature (Paine et al. 2012).

279   Given the importance of habitat filtering on seedling survival, we then built a habitat-only model,

280   including habitat variables in addition to initial seedling height (Table 1, Appendix 1). To assess

281   the role of neighbor densities on seedling survival, we then built models in which conspecific

282   and heterospecific neighbor effects were included together and separately. In these density-

283   dependent models, seedling survival depended on initial seedling height, the total seedling

284   neighbor density or conspecific and heterospecific seedling neighbor densities, and the total adult

285   neighbor density or conspecific and heterospecific adult neighbor densities (Table 1, Appendix

286   1). To assess the importance of evolutionary relationships in the survival model, we finally

287   constructed phylogenetic density-dependent models in which heterospecific neighbor densities

288   were replaced by the phylogenetic diversity indices described above (Table 1, Appendix 1).

289   Akaike's Information Criterion (AIC) was used to compare models, with ΔAIC calculated

290   by subtracting the overall minimum value of AIC from each of the models' AIC values. We

291   selected the most parsimonious models among those with $\varDelta$AIC less than 2, which are thought to

292   be the equally best-fitting models (Burnham and Anderson 2002). We identified the best-fitting

293   density-dependent model (Table S4) and the best-fitting phylogenetic density-dependent model

294   (Table S5).

295   To explore the influence of habitat filtering on the detection of CNDD and PNDD, we

296   compared the best-fitting density-dependent model to the equivalent model in which habitat

297   variables were included (density + habitat model) (Table 1, Appendix 1). We also compared the

298   best-fitting phylogenetic density-dependent model with its equivalent phylogenetic + habitat

299   model (Table 1, Appendix 1). We also included interactions between habitat variables and

300   neighborhood variables and used AIC scores to identify the best interaction terms combination in

301   both the 'density + habitat' model (Table S6) and the 'phylogenetic + habitat' model (Table S7).

302   In total, we ran six classes of model: (1) density-independent; (2) habitat-only; (3) density-

303   dependent; (4) density + habitat; (5) phylogenetic density-dependent and (6) phylogenetic +

304   habitat. Equations defining these models can be found in Appendix 1.

305   We analyzed the above six model classes for each of the four one-year census intervals

306   (Table 1). To explore the effects of habitat filtering on the detection of CNDD and PNDD, we

307   compared the estimated coefficients of neighborhood variables in four of our models: the best-

308   fitting density-dependent model (model I in Table 2), the density + habitat model with the same

309   neighborhood variables as in the best-fitting density-dependent model (model II in Table 2), the

310   best-fitting phylogenetic density-dependent model (model III in Table 2) and the phylogenetic +

311   habitat model with the same neighborhood variables as in the best-fitting phylogenetic density-

312   dependent model (model IV in Table 2). We labelled models I and II as 'density models', and

313   models III and IV as 'phylogenetic models'. The estimated coefficients represent the relative

314   strength of the variables' effects, and coefficients > 0 indicate positive effects on seedling

315   survival while coefficients < 0 indicate negative effects. Specifically, a positive estimated

316   coefficient for phylogenetic diversity indices indicates a negative relationship between the

317   phylogenetic similarity of heterospecific neighbors and seedling survival (and vice versa). We

318   calculated the variance for each of the models' fixed effects, random effects and for the residuals

319   in each of the above four models (Table S8).

320   To determine whether and how habitat filtering affects the detectability of CNDD and

321   PNDD among species, we added species-specific random slopes for each neighborhood variable

322   in the above four models. Differences between these slopes within a model, and across models

323   with and without habitat variables, were used to capture species-specific responses to neighbor

324   densities and the extent to which habitat filtering might obscure these responses. We used

325   likelihood ratio tests to assess the significance of added species-specific random slopes (Table

326   S9). If P values were less than 0.05, we inferred that the coefficients of neighborhood variables

327   did vary across species. We also used two-sample Kolmogorov-Smirnov tests to compare the

328   distributions of the species-specific coefficients of neighborhood variables between the varying-

329   slope models with and without habitat variables.

330

331   **RESULTS**

332   CNDD, PNDD and habitat filtering for seedling survival in the best-fitting model

333   In the 414 target seedling quadrats, there were 8324, 7868, 7680 and 8156 living seedlings of

334   238, 237, 240 and 262 focal woody plant species in the 2010, 2011, 2012 and 2013 censuses

335   respectively.

336   Of the six survival models we built, the phylogenetic + habitat model had the best-fit for the

337   2011-2012 and 2013-2014 census intervals, while the density + habitat model and habitat-only

338   model had the best-fit for 2010-2011 and 2012-2013 respectively (Table 1). Across all four

339   census intervals, seedling survival was mainly influenced by fixed effects for habitat variables,

340   followed by the density of conspecific seedling and adult neighbors and NTPd' of heterospecific

341   seedling and adult neighbors (Fig. 1). The effects of the first principal component of topographic

342   and edaphic variables were significantly positively correlated with seedling survival for three

343   census intervals (2010-2011, 2011-2012 and 2013-2014), whereas canopy openness was

344   significantly negatively related for the 2012-2013 census interval. Conspecific adult neighbors

345   had significantly negative effects on survival for the first three census intervals (Table 2). Across

346   all four census intervals, seedling and adult NTPd' generally had insignificant negative effects.

347

348   How does habitat filtering affect the detection of CNDD?

349   Across all four census intervals, the coefficients of conspecific seedling and adult neighbor

350   densities were smaller in Models I and III (without habitat variables) than in Models II and IV

351   (with habitat variables) (Table 2). There were also significant positive interactions between

352   habitat variables and conspecific seedling and adult neighbor densities in Models II and IV

353   (Table 2). Furthermore, we found that adding habitat variables increased the variance explained

354   by the densities of conspecific seedling and adult neighbors, while variances explained by

355   random effects remained almost constant (Table S8). Together, these results indicate that the true

356   extent of CNDD was obscured when not accounting for habitat variables.

357   Because adult CNDD was significant in the best-fit models for 2010-2011 and 2011-2012

358   (Table 2), we added species-specific random slopes for conspecific adult neighbor density to

359   these models. The distribution of these species-specific coefficients changed significantly

360   between models with and without habitat variables (Models II and IV vs. I and III; two-sample

361   Kolmogorov-Smirnov test, $p < 0.05$, Fig. 2). When taking into account habitat variables in

362   Model II, we found that 97.90% and 97.47% of the focal species in the 2010-2011 and 2011-

363   2012 census intervals suffered stronger negative effects of conspecific adult neighbor densities

364   than those in equivalent non-habitat informed models (Model I). Similarly, 98.32% and 92.83%

365   of the focal species in Model IV (with habitat variables) suffered stronger negative effects than

366   those in model III (without habitat variables).

367

368   How does habitat filtering affect the detection of PNDD?

369   Across all four census intervals, the coefficients of seedling NTPd' and adult NTPd' were

370   generally negative in both Models III (without habitat variables) and IV (with habitat variables)

371   (Table 2), indicating that seedlings survived significantly better when growing among closely

372   related heterospecific neighbors. In contrast to conspecific neighbor densities, adding habitat

373   variables into the survival models did not substantially affect the coefficients of the phylogenetic

374   diversity indices, and the interactions between habitat variables and s_NTPd' and a_NTPd' were

375   insignificant (Table 2). The inclusion of species-specific random slopes for seedling NTPd' and

376   adult NTPd' did not significantly increase the variation explained (Table S9). Thus, we did not

377   conduct further analyses into how habitat filtering affected the variation of PNDD among

378   species.

379

380   **DISCUSSION**

381   Conspecific negative density dependence (CNDD), phylogenetic negative density dependence

382   (PNDD) and habitat filtering are often cited as prominent mechanisms maintaining the

383   composition and diversity of communities. Some studies have discussed a potentially

384   confounding influence of habitat filtering when attempting to quantify negative density

385   dependence (Comita et al. 2009, Chen et al. 2010, Bai et al. 2012, Piao et al. 2013), but this has

386   not previously been well documented. Our results show that CNDD and habitat filtering

387   simultaneously influence seedling survival. Taking habitat variables into account elucidated more

388   clearly the negative impacts of conspecific neighbors (seedlings + adults) on seedling survival,

389   and made the species-specific negative effects of conspecific neighbor densities generally

390   stronger. Our study system showed the opposite effect with respect to PNDD. In the following

391   we discuss these results in more detail.

392

393   Local neighborhood and habitat effects

394   Seedling-seedling and seedling-adult interactions may be stronger in tropical forests than in

395   subtropical forests (e.g., Chen et al. 2010) or temperate forests (e.g., Bai et al. 2012). We found

396   these interactions, at the scales we considered, were a significant driver of seedling survival.

397   These results are in line with evidence from other tropical forests (e.g., Queenborough et al.

398   2007, Comita et al. 2009, 2010, Metz et al. 2010, Kobe and Vriesendorp 2011, Johnson et al.

399   2012, Lebrija-Trejos et al. 2014). The negative effects of conspecific neighbors on seedling

400   survival are consistent with intraspecific competition and the Janzen-Connell hypothesis (Janzen

401   1970, Connell 1971). Our results show that seedling survival was significantly influenced by

402   densities of conspecific seedling and adult neighbors, which may be involved in intraspecific

403   competition for shared resources and/or as a source for specialized natural enemies (herbivore

404   and pathogen) (e.g., Augspurger 1984, Packer and Clay 2000, 2003, Bell et al. 2006, Freckleton

405   and Lewis 2006, McCarthy-Neumann and Kobe 2008). Another possible explanation for the

406   negative impact of conspecific adult neighbors is that their presence implies that there may be

407   many more conspecific seedling neighbors over the wider area (beyond our seedling quadrats),

408   making competition and mortality due to pests and pathogens even greater than we expect from

409   measured seedling densities.

410   Recently, several studies focusing on NDD for seedling survival have scaled the effects of

411   heterospecific neighbors by phylogenetic relatedness. For example, Liu et al. (2012) found a

412   phylogenetic Janzen-Connell effect, which might be caused by associated host-specific fungal

413   pathogens in a subtropical forest. Metz et al. (2010) found that seedling survival increased where

414   nearby adult neighbors were more distantly related to focal seedlings. The critical factors

415   affecting a pathogen's infection of a host plant are morphological and biochemical, which are

416   often phylogenetically conserved (Mitter et al. 1991). Further, empirical evidence has shown that

417   closely related species are more likely to share the same or similar pests and pathogens (e.g.,

418   Novotny et al. 2006, Gilbert and Webb 2007, Gilbert et al. 2012, Liu et al. 2012), and to have

419   several similar key functional traits (Yang et al. 2014). Thus, the effects of neighbors on a focal

420   plant should depend upon phylogenetic similarities, and should be less negative for less related

421   plants. However, we found a negative effect of phylogenetic diversity, indicating that increased

422   phylogenetic similarities between heterospecific neighbors and focal seedlings increased

423   seedling survival. Our results therefore do not support PNDD. While these findings are in

424   contrast to those of the studies cited above, they are consistent with several other studies that

425   have shown that plants perform better when heterospecific neighbors are relatively closely

426   related (summarized in Lebrija-Trejos et al. 2014). Our results also suggest that this phylogenetic

427   positive density-dependence (PPDD) is a more important determinant of seedling survival than

428   PNDD (see below).

429   The edaphic and topographic variables in our study had important effects on seedling

430   survival. Specifically, the positive effect of the first principal component of edaphic and

431   topographic variables on seedling survival demonstrated that the availability of below-ground

432   resources is also an important driver of tree seedling survival (Comita et al. 2009, Bai et al. 2012,

433   Piao et al. 2013). Many works have also shown that light availability has a strong effect on the

434   performance of shade-tolerant seedlings in tropical forests (e.g., Paz and MartÍnez-Ramos 2003,

435   Comita et al. 2009, Queenborough et al. 2009). However, light availability had a slight negative

436   effect on seedling survival in our study, even though the range of canopy openness we found was

437   sufficient to produce positive effects (with approximately 90% of seedling quadrats within a

438   range of canopy openness between 0.29% and 3%). This unexpected relationship may indicate a

439   widespread problem with the use of canopy photographs in studies of this kind (e.g., Comita et

440   al. 2009; Lin et al. 2014).

441

442   Habitat filtering and CNDD

443   The increase in survival driven by favorable habitat may offset the thinning of conspecific trees

444   due to CNDD (Wright 2002). A positive relationship with conspecific densities would therefore

445   be found when host-specific natural enemies or intra-specific competition do not offset the

446   advantages of occurring in a preferred habitat (at least until the population size becomes too

447   large). A few studies have shown such an interaction between habitat variables and negative

448   density dependence. For example, Piao et al. (2013) suggested that a failure to take into account

449   the confounding effect of habitat heterogeneity may lead to mischaracterization of the role of

450   density dependence in shaping plant communities. Zhu et al. (2010) found that factoring out

451   habitat heterogeneity made most tree species show negative density dependence in a subtropical

452   forest, but did not explore in detail exactly how habitat variables affected density dependence.

453   Our work clearly shows that taking habitat variables into consideration made the effects of

454   conspecific neighbors appear more negative in both the density models and the phylogenetic

455   models (Table 2). The significant positive interactions between habitat variables and conspecific

456   seedling and adult neighbor densities (Table 2) implied changes in CNDD across different habitat

457   conditions. This is why the variance explained by the densities of conspecific seedling and adult

458   neighbors increased in models with habitat variables (Table S8).

459   The impact of habitat filtering on the detection of CNDD can also be seen in the prevalence of

460   species-habitat associations at both seedling and adult stages in the XSBN plot (Table S10). Of

461   the species with more than 20 surveyed seedlings, 41.77% and 60.76% showed significant

462   habitat preferences at the seedling stage and the adult stage, respectively. Our results therefore

463   suggest that conspecific negative density dependence is evident at lower densities in marginal

464   habitats and only at higher densities in optimal habitats. Further, the inclusion of habitat

465   variables led to an increase in apparent strength of species-specific negative effects of

466   conspecific neighbors, especially conspecific adult neighbors. In sum, CNDD and habitat

467   filtering both had vital influences on seedling dynamics and the observed effects of conspecific

468   neighbors were the result of an interaction between them.

469   Lack of evidence for PNDD

470   Though more and more ecologists have concluded that phylogenetic density dependence is an

471   important mechanism for seedling dynamics and coexistence (e.g., Webb et al. 2006, Metz et al.

472   2010, Zhu et al. 2015), the influence of habitat filtering on the detection of phylogenetic density

473   dependence had not been taken into account. As with conspecifics, the impact of natural enemies

474   and the stronger competition for similar resources among closely related neighboring plants

475   should lead to a negative effect of phylogenetic similarity on seedling survival. An apparently

476   positive relationship between phylogenetic similarity and seedling survival might be caused by

477   habitat filtering, because closely related plants may often have similar habitat requirements

478   (Vamosi et al. 2009, Baldeck et al. 2013). We expected that habitat filtering could therefore affect

479   the detection of the negative effect of phylogenetic similarity on seedling survival in the same

480   way that it affected CNDD detectability. However, this expectation was not met in this study.

481   While we did find that the inclusion of phylogenetic relatedness of heterospecific neighbors

482   improved model accuracy, we found no evidence of PNDD. Furthermore, differences in the

483   effects of phylogenetic relatedness between survival models without and with habitat variables

484   were relatively slight. Instead, we found evidence of phylogenetic positive density-dependence

485   (PPDD). There appears to be an emerging consensus about the existence of this effect, perhaps

486   due to the shared habitat preferences between closely related individuals (Lebrija-Trejos et al.

487   2014). However, our results showed that seedling survival was greater among closely related

488   heterospecific neighbors even when habitat variation was controlled (Model IV in Table 2).

489   While it is possible that unobserved habitat factors had a confounding effect on this analysis, it is

490   not clear what these factors might be, and it seems unlikely that they could be strong enough to

491   reverse the apparent direction of relationships between seedling survival and neighbor

492   relatedness. We therefore suggest that PPDD, as detected here, may be a real and independent

493   effect of some as-yet unrecognized mechanism.

494

495   **CONCLUSIONS**

496   To the best of our knowledge, our study is the first to explore the joint effects of conspecific

497   negative density-dependence (CNDD), phylogenetic negative density-dependence (PNDD) and

498   habitat filtering and their relative importance for tropical tree seedling survival. Our results

499   demonstrate that replacing heterospecific neighbor densities with phylogenentic diversity indices

500   improved survival models, which is in line with an increasing awareness of the importance of

501   evolutionary relationships in neighborhood dynamics. However, the effect of phylogenetic

502   diversity indices in our study system was opposite to that expected under PNDD, even when we

503   controlled for the effects of habitat. CNDD and habitat filtering played important roles in

504   seedling survival simultaneously. The observed effect of conspecific neighbor densities is

505   primarily a result of an interaction between habitat filtering and conspecific neighbor densities,

506   making CNDD detectable at lower densities in marginal habitats than in preferred habitats.

507   Therefore, adding habitat variables into survival models strengthens the measured negative

508   effects of conspecific neighbors on seedling survival. We conclude that future studies of

509   neighborhood density dependence must take habitat filtering and phylogenetic relationships into

510   account in order to properly assess the effects of conspecific and heterospecific neighbors, and

511   the occurrence and cause of phylogenetic positive density-dependence.

512   **ACKNOWLEDGEMENTS**

526

527

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707

708

709   TABLES

710   TABLE 1. AIC values for the six classes of model for each of the four one-year census intervals.

Candidate model	AIC			
	2010-2011	2011-2012	2012-2013	2013-2014
Density-independent model				
H	3463.1	3213.7	4227.3	4997.7
Habitat-only model				
H+ light+ PCA1+ PCA2	3448.3	3203.9	**4225.2**	4998.8
Density-dependent model[†]				
H + cons+hets +CA+ HA	3462.6	3214.8	4230.2	5003.1
Density +habitat model[††]				
H + cons+hets +CA+ HA +light+ PCA1+ PCA2+cons×PCA1+ cons×PCA2+CA×PCA1+ CA×PCA2	**3442.0**	3201.9	4234.0	4998.2
Phylogenetic density-dependent model[‡]				
H +cons+ s_NTPd'+CA+a_ NTPd'	3466.0	3211.4	4230.1	5000.4
Phylogenetic +habitat model[§]				

H +cons+ s_ NTPd'+CA+a_ NTPd'+light + PCA1+ PCA2+ cons×PCA1+cons×PCA2+ CA×PCA1+ CA×PCA2+s_ NTPd' ×PCA1+ s_ NTPd' ×PCA2+ a_ NTPd' ×PCA1+ a_ NTPd' ×PCA2	3449.1	**3196.9**	4234.7	**4996.6**

711 [†]The model comparison for density-dependent models is shown in Table S4. [††]The model

712 comparison for density + habitat models with different interaction term combinations is shown in

713 Table S6. [‡]The model comparison for phylogenetic density-dependent models is shown in Table

714 S5. [§]The model comparison for phylogenetic+habitat models with different interaction

715 combinations is shown in Table S7. 'H' is the heights of focal seedlings. Neighborhood variables

716 included the density of conspecific seedling neighbors (cons), the density of heterospecific

717 seedling neighbors (hets), sum of conspecific adults' basal areas weighted by the distance

718 between the focal seedling and the adult neighbors at distances up to 20 m (CA), sum of

719 heterospecific adults' basal areas weighted by the distance between the focal seedling and the

720 adult neighbors at distances up to 20 m (HA), and two phylogenetic diversity indices: relative

721 nearest taxon phylogenetic diversity between heterospecific seedling neighbors and focal

722 seedlings (s_NTPd') and relative nearest taxon phylogenetic diversity between heterospecific

723 adult neighbors and focal seedlings (a_NTPd'). Habitat variables included canopy openness %

724 (light) and the first two principal components (PCA1and PCA2) of soil properties and

725 topography. ΔAIC is calculated by subtracting the minimum AIC value from each of AIC values

726 of the models. We selected the most parsimonious models among the models with ΔAIC ≤ 2

727 (AIC in bold) (Table S2).

728 TABLE 2. Coefficient estimates for all explanatory variables in the density-dependent model (Model I), the density + habitat model

729 with the same neighborhood variables as that in the density-dependent model (Model II), the phylogenetic density-dependent model

730 (Model III) and the phylogenetic + habitat model with the same neighborhood variables as that in the phylogenetic density-dependent

731 model (Model IV), for each of the four one-year census intervals.

Explanatory variables	2010-2011				2011-2012				2012-2013				2013-2014			
	I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV
Intercept	3.686***	3.640***	3.663***	3.601***	3.616***	3.581***	3.584***	3.514***	2.849***	2.830***	2.827***	2.811***	2.691***	2.633***	2.644***	2.599***
Height	0.698***	0.678***	0.696***	0.678***	0.783***	0.779***	0.783***	0.748***	0.323***	0.318***	0.322***	0.314***	-0.037NS	-0.037NS	-0.037NS	-0.038NS
cons	0.095NS	0.006NS	0.042NS	-0.019NS	0.076NS	-0.038NS	0.075NS	-0.022NS	0.071NS	0.042NS	0.052NS	0.034NS	-0.010NS	-0.115NS	-0.029NS	-0.125NS
hets	0.159NS	0.088NS			0.002NS	-0.059NS			0.054NS	0.050NS			0.047NS	0.026NS		
CA	-0.110*	-0.169**	-0.116*	-0.187**	-0.127*	-0.166**	-0.125*	-0.185**	-0.091*	-0.113NS	-0.090*	-0.117*	-0.055NS	-0.095NS	-0.052NS	-0.093NS
HA	0.002NS	0.035NS			0.003NS	0.020NS			-0.026NS	-0.010NS			-0.061NS	-0.045NS		
s_NTPd'			-0.029NS	-0.025NS			-0.100NS	-0.137*			-0.016NS	-0.055NS			-0.016NS	-0.024NS
a_ NTPd'			-0.034NS	0.001NS			-0.083NS	-0.028NS			-0.071NS	-0.059NS			-0.157NS	-0.140NS

light	-0.084NS	-0.076NS	-0.025NS	-0.020NS	-0.177**	-0.170*	-0.059NS	-0.065NS
PCA1	0.328***	0.314***	0.299***	0.272***	0.117NS	0.106NS	0.197**	0.201**
PCA2	0.261**	0.245**	0.202**	0.143NS	0.103NS	0.106NS	0.025NS	0.038NS
cons×PCA1	0.103NS	0.084NS	0.056NS	0.053NS	0.069NS	0.056NS	0.118NS	0.121NS
cons×PCA2	0.029NS	0.011NS	0.167*	0.138NS	-0.001NS	-0.015NS	0.004NS	0.011NS
CA×PCA1	0.150*	0.133NS	0.072NS	0.088NS	0.041NS	0.035NS	0.164**	0.165**
CA×PCA2	0.224**	0.212**	0.052NS	0.055NS	0.021NS	0.022NS	0.089NS	0.083NS
s_NTPd' ×PCA1		0.059NS		0.032NS		0.020NS		-0.082NS
s_NTPd' ×PCA2		0.016NS		0.128*		0.115*		0.063NS
a_NTPd' ×PCA1		0.017NS		0.073NS		0.044NS		0.011NS
a_NTPd' ×PCA2		0.051NS		0.093NS		-0.041NS		-0.086NS

732　* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, not significant. See Table 1 for variable abbreviations.

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734   Figure Legends

735

736   FIG. 1. Estimated effects (± 2SE) of neighborhood variables and habitat variables on seedling

737   survival for each of the four one-year census intervals in phylogenetic + habitat model (Model IV

738   in Table 2). Filled circles indicate significant effects ($P < 0.05$). The interactions of neighborhood

739   variables and habitat variables were not shown here and can be found in Table 2. See Table 1 for
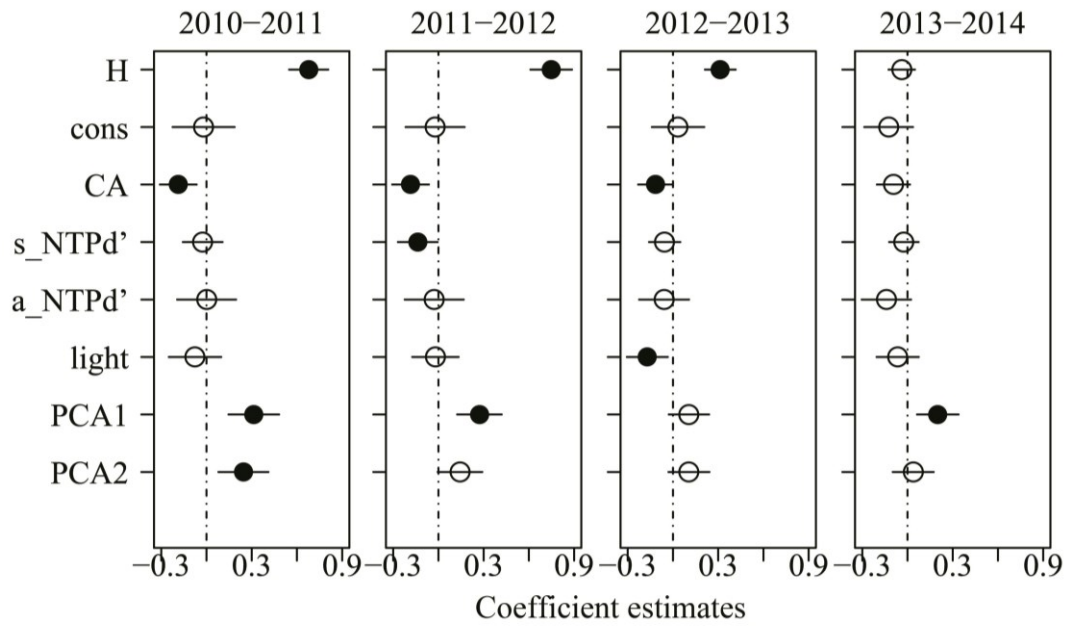
740   variable abbreviations.

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742   FIG. 2. A comparison of the frequency distribution of species-specific coefficients of conspecific

743   adult neighbor density between model I (Density model without habitat variables) and model II

744   (Density model with habitat variables), and between model III (Phylogenetic model without

745   habitat variables) and model IV (Phylogenetic model with habitat variables) for 2010-2011 and

746   2011-2012 census intervals. Bars to the left of the dashed zero line indicate species whose survival

747   is reduced by increasing neighborhood variables.

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