1

6   *Title:* Interspecific variation in conspecific negative density dependence can make species

7   less likely to coexist

8   *Running title:* Variable CNDD undermines coexistence

9

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41 **Abstract**

42 Conspecific negative density dependence (CNDD) is thought to promote plant species

43 diversity. Theoretical studies showing the importance of CNDD often assumed that all

44 species are equally susceptible to CNDD; however, recent empirical studies have shown

45 species can differ greatly in their susceptibility to CNDD. Using a theoretical model, we

46 show that interspecific variation in CNDD can dramatically alter its impact on diversity.

47 First, if the most common species are the least regulated by CNDD, then the stabilizing

48 benefit of CNDD is reduced. Second, when seed dispersal is limited, seedlings that are

49 susceptible to CNDD are at a competitive disadvantage. When parameterized with

50 estimates of CNDD from a tropical tree community in Panama, our model suggests that

51 the competitive inequalities caused by interspecific variation in CNDD may undermine

52 many species' ability to persist. Thus, our model suggests that variable CNDD may make

53 communities less stable, rather than more stable.

54

55 **Introduction**

56 The Janzen-Connell hypothesis is a leading theory for how trees coexist, especially in

57 highly diverse tropical forests (Wright 2002; Carson *et al.* 2008; Terborgh 2012; Comita

58 *et al.* 2014). It proposes that trees coexist because specialized natural enemies reduce

59 seeds' and seedlings' survival when conspecific densities are high (Janzen 1970; Connell

60 1971), resulting in an effect called conspecific negative density dependence (CNDD).

61   The hypothesis claims that rare species have more CNDD-free areas than common

62   species; therefore, rarer seedlings survive better than common seedlings, preventing any

63   species from becoming too common or too rare (Janzen 1970; Connell 1971). This 'rare

64   species advantage' thereby maintains diversity by reducing the likelihood that rare

65   species are lost from the community (Chesson 2000). CNDD has been shown to promote

66   species diversity at small scales (e.g., <15 m^2), and this has been extrapolated to suggest

67   that CNDD promotes diversity at the community level (Harms *et al.* 2000; Bagchi *et al.*

68   2014).

69

70   Recent studies have added a new twist to the Janzen-Connell hypothesis: species differ in

71   their responses to conspecific neighbor density (Klironomos 2002; Petermann *et al.* 2008;

72   Comita *et al.* 2010; Mangan *et al.* 2010; Kobe & Vriesendorp 2011; Reinhart 2012; Zhu

73   *et al.* 2015; Johnson *et al.* 2017; Murphy *et al.* 2017). For example, invasive species

74   (Klironomos 2002), shade tolerant species (Kobe & Vriesendorp 2011), slow-growing

75   species (Zhu *et al.* 2018), and species with high resistance gene diversity (Marden *et al.*

76   2017) have been shown to be less sensitive to conspecific neighbors and therefore less

77   susceptible to CNDD. Several studies have also shown that conspecific neighbors tend to

78   be more harmful for rarer species compared to species that are more common in the

79   community (Klironomos 2002; Petermann *et al.* 2008; Comita *et al.* 2010; Mangan *et al.*

80   2010, though for exceptions see Reinhart 2012; Zhu *et al.* 2015; Wills *et al.* 2016). Thus,

81   the picture becomes more complex: common species are exposed to higher densities of

82   conspecifics than rare species, but if they are relatively insensitive to those neighbors,

83   then CNDD may not translate into higher seedling mortality for common species. If this

84   weakens the 'rare species advantage,' then CNDD will be less able to maintain diversity

85   (Chesson 2000).

86

87   Despite the many empirical studies testing for CNDD (Comita *et al.* 2014), theoretical

88   work on the topic has lagged behind. Theoretical models are essential for understanding

89   the long-term, community-level consequences of CNDD, because trees are too large and

90   long-lived to be amenable to multi-generational manipulations. Theoretical studies have

91   shown that CNDD promotes diversity (Leigh 1982; Armstrong 1989; Adler & Muller-

92   Landau 2005; Muller-Landau & Adler 2007; Stump & Chesson 2015); however, these

93   models did not include variation among species in their sensitivity to conspecific

94   neighbors. Models that incorporated interspecific variation in CNDD focused mainly on

95   the implications for species abundance (Mangan *et al.* 2010; Chisholm & Muller-Landau

96   2011; Mack & Bever 2014). They generally concluded that higher susceptibility to

97   CNDD causes species to have lower abundance in the community (Mangan *et al.* 2010;

98   Chisholm & Muller-Landau 2011; Mack & Bever 2014). Miranda et al. (2015) took this a

99   step further, showing that variation in CNDD leads to variation in abundances and even

100   extinctions, both of which reduce diversity (based on the Shannon index). However, the

101   implications of species differences in CNDD for species coexistence have yet to be fully

102   explored.

103

104   Variation among species in CNDD may influence coexistence through several processes.

105   First, differential susceptibility to natural enemies could create stabilizing mechanisms,

106   but it could also create competitive differences that can undermine coexistence (Stump &

107   Chesson 2017). Second, factors that make species rare make them more susceptible to

108   demographic stochasticity (Nisbet & Gurney 1982). Thus, variable CNDD that causes

109   some species to be rare would likely lead to extinctions. However, it is not clear whether

110   rarity due to CNDD has different consequences than rarity that results from other factors

111   (e.g., overall competitive ability). Finally, the influence of variation in CNDD will likely

112   depend on patterns of seed dispersal, as limited dispersal greatly affects the impact of

113   CNDD (Muller-Landau & Adler 2007; Murrell 2010; Stump & Chesson 2015).

114

115   In this paper, we use a theoretical model to examine how variation in susceptibility to

116   CNDD affects community stability and diversity. Our results suggest that communities

117   are usually less stable if rare species suffer stronger CNDD, particularly when seed

118   dispersal is low. We also show that variation in sensitivity to CNDD is more harmful to

119   coexistence than variation in many other competitive factors. Additionally, we

120   parameterize our model using estimates of CNDD from tree species in the lowland

121   tropical forest of Barro Colorado Island (BCI), Panama. Our results suggest that many

122   species on BCI are being excluded from the community by CNDD, rather than

123   maintained by it.

124

125   **Model & Analysis**

126   We modeled forest dynamics using a site-occupancy model, based on Stump and

127   Chesson (2015) and Chisholm and Muller-Landau (2011). Parameters are listed in Table

128   1. The forest contains a fixed number of sites, each of which contains 1 adult. Seeds

129   compete for empty gaps, and a seed's chance of capturing a gap is affected by CNDD.

130

131   Four processes occur each time step. First, adults produce and disperse seeds (Fig. 1a).

132   A fraction d of seeds are dispersed uniformly around the environment, and the remaining

133    $(1–d)$ stay at their parent's site. Second, seeds are harmed by CNDD (Fig. 1b). If a seed

134   does not disperse, or if it disperses to a site held by a conspecific adult, then it dies with

135   probability α_j (for species j); otherwise, it survives with probability 1. Third, each adult

136   dies with probability δ (Fig. 1c). If an adult survives, then all of the seeds that dispersed

137   to its site die. Finally, one seed is chosen randomly to become the adult by the next time

138   step (Fig. 1d) (i.e., lottery competition, Chesson & Warner 1981).

139

140   We wanted to consider the possibility that a species could be more or less competitive

141   due to factors other than CNDD. To do this, we assume that a species' chance of being

142   chosen to capture a gap is proportional to its yield, Y_j for species j (Chisholm & Muller-

143   Landau 2011; Stump & Chesson 2015). A high Y_j can represent an adult producing more

144   seeds, those seeds being more competitive, those seeds having high density-independent

145   survival, or a combination of effects. Thus, a species with a high Y_j has an advantage in

146   capturing all sites, whereas a species with a low α_j has a relative advantage in capturing

147   conspecific sites.

148

149   Together, the competition-weighted number of seeds competing for a site that was

150   previously held by species j is

$$C_j = Y_j\big(1 - d + dN_j\big)\big(1 - \alpha_j\big) + \sum_{k \neq j} Y_k dN_k \,,$$

151   (1)

152   where N_j is the fraction of sites held by species j, and the summation is over all species

153   except species j (Appendix: Analytical results). The finite rate of increase (discrete-time

154   growth rate) of species j is

$$\tilde{\lambda}_j = (1 - \delta) + \frac{\delta Y_j (1 - d)(1 - \alpha_j)}{C_j} + \delta Y_j d \left(\frac{N_j (1 - \alpha_j)}{C_j} + \sum_{k \neq j} \frac{N_k}{C_k} \right)$$

155   (2)

156   (Appendix: Analytical results). The first term in eqn (2) is adult survival, the second term

157   is the probability that a non-dispersed seed captures its parent's site, and the third term is

158   the number of sites captured by dispersed seeds (held by conspecific and heterospecific

159   adults, respectively).

160

161   *Model analysis*

162   We determined if communities are deterministically stable using invasion analysis

163   (Turelli 1978; Chesson 2000). Each species was selected in turn to be an invader

164   (denoted with subscript i), and its density was set to approximately 0. We let the other

165   species come to equilibrium. We then calculated each invader's finite rate of increase,

166   weighted by its sensitivity to competition ($\tilde{\lambda}'_j$). We partitioned $\tilde{\lambda}'_j$ into terms caused by

167   CNDD, ΔP_j, and terms caused by yield, ΔY_j (Appendix: Analytical results). The

168   stabilizing mechanisms were quantified as the mean of each term, $\overline{\Delta P}$ and $\overline{\Delta Y}$, and the

169   mean fitness-difference between species j and its competitors was quantified as the

170   difference from average, $\left(\Delta P_j - \overline{\Delta P} \right)$ and $\left(\Delta Y_j - \overline{\Delta Y} \right)$ (Chesson 2003). Thus, there is one

171   stabilizing effect for each community, but each species has a mean fitness-difference

172   describing its competitive ability (Chesson 2003). We quantified stability for particular

173   parameter sets by simulating the model using Matlab (The MathWorks Inc. 2017).

174

175   We determined how robust communities are to demographic stochasticity using

176   simulations (Appendix: Computer simulations). Species competed in small, closed

177   communities (typically 2000 sites). Communities were seeded with species at their

178   equilibrium density, which was calculated in a much larger community. In communities

179   where some species could not persist in a deterministic setting, the initial density was set

180   to 1% of sites (to measure the speed of exclusion). We simulated community dynamics

181   for 2000 generations. We determined both ln{time to first extinction} (which was

182   ln{2000} if no species went extinct), and the number of species remaining after 2000

183   generations. We repeated this process 5000 times to determine the average.

184

185   *Parameterizing our model*

186   We parameterized our model using data from Comita *et al.* (2007) and Comita *et al.*

187   (2010). In Comita *et al.* (2010), hierarchical Bayesian models were used to study

188   predictors of seedling survival over 5 years in 20,000 1-m^2 seedling plots in the 50-ha

189   Forest Dynamics Plot on BCI, Panama. For our analysis, we considered only canopy tree

190   species (as classified in Comita *et al.* 2007) and eliminated any species that did not have

191   at least 1 reproductive adult in the plot. This left us with 77 species.

192

193   As we show below, three parameters are needed to estimate the impact of CNDD: each

194   species' sensitivity to CNDD (α_j), the frequency of each species in the community (N_j),

195   and the fraction of seeds dispersed (*d*). We parameterized α_j using the parameter

196   CONBA in Comita *et al.* (2010), which estimated how seedling survival decreased as a

197   function of the distance-weighted basal area of conspecific adults (specifically weighted

198   by exp{–0.2*distance}). Thus, CONBA was not exactly the same as –α_j, though we felt

199   it was adequate for our purposes. Our results were slightly stronger when we

200   parameterized models using CONS (the impact of conspecific seedlings on survival)

201   from the same study. We considered two possible measurements of N_j: total basal area

202   (Comita *et al.* 2010) and the number of reproductive adults (Comita *et al.* 2007). In each

203   case, N_j was the fraction of a species' basal area or abundance divided by the total basal

204   area or abundance of the canopy trees considered. We could not confidently parameterize

205   dispersal, so we considered a wide range of possibilities.

206

207   Code and data are available at the Dryad Digital Repository:

208   http://dx.doi:10.5061/dryad.dr34q6v.

209

Results

210

211 Our results follow from a simple principle: seed and seedling mortality is harmful.

212 Therefore, if one species suffers higher mortality than others, then it is at a disadvantage,

213 and could potentially be outcompeted by species who suffer lower mortality. However, if

214 mortality is frequency-dependent, such that species survive better when they become

215 rare, then such mortality can potentially offset any disadvantages, allowing weaker

216 competitors to coexist with stronger competitors (Chesson 2000). Thus, much of our

217 analysis involves quantifying how much of an advantage a rare species can get because of

218 frequency-dependent mortality, and whether it is enough to counteract any inherent

219 differences in survival or competitiveness.

220

221 We first show how variation in susceptibility to CNDD (α_j) affects stability, all else being

222 equal. Second, we compare the effect of differences in α_j to differences in yield (Y_j).

223 Third, we present results from our model that suggest methods for quantifying the impact

224 of CNDD. Finally, we use those methods to examine the effect of CNDD on BCI.

225

226 *How does variation in CNDD affect diversity and stability?*

227 If there is no interspecific variation in CNDD, then our model reproduces the same 'rare

228 species advantage' of previous models (Leigh 1982; Armstrong 1989; Adler & Muller-

229 Landau 2005; Muller-Landau & Adler 2007; Chisholm & Muller-Landau 2011; Stump &

230 Chesson 2015): a species who becomes rare has fewer sites where it experiences CNDD,

231 and thus it experiences lower seedling mortality than its more common competitors. The

232 benefit of CNDD is proportional to the amount that mortality is reduced for an invader

233 compared to species at equilibrium (ΔP_j). The stabilizing effect of CNDD is quantified as

234 the mean of ΔP_j across species, $\overline{\Delta P}$ (Chesson 2003). If CNDD does not vary (i.e., $\alpha_j = \bar{\alpha}$

235 for all species, where $\bar{\alpha}$ is the mean of α_j across species), then a community with S

236 species will have a stabilizing mechanism of

$$\overline{\Delta P} \approx \frac{d^2 \bar{\alpha}}{S-1}$$

237 (3)

238 (Stump & Chesson 2015) (Appendix: Analytical results). If there are no other differences

239 among species, then the system has a stabilizing mechanism and no fitness-differences,

240 and thus will be strongly stabilized (Chesson 2000).

241

242 Variation in CNDD usually weakens the 'rare species advantage' (i.e., reduces the

243 stabilizing effect, Fig. 2b). Species still have increased seedling survival when they

244 become rare; however, if the most common species are tolerant of CNDD, then the

245 difference in survival will be smaller. As a result, the benefit to becoming rare is reduced.

246 We found that when CNDD varies, $\overline{\Delta P}$ depends on each species' frequency (N_j):

$$\overline{\Delta P} \approx d^2 \left(\frac{\bar{\alpha}}{S-1} + \text{cov}(\alpha_j, N_j) \right)$$

247   (4)

248 where the covariance is taken at equilibrium (Appendix: Analytical results). The

249 covariance term arises from the difference between $\bar{\alpha}$ and the abundance-weighted mean

250 of α_j. It will be negative –and $\overline{\Delta P}$ will be reduced– if common species are less susceptible

251 to CNDD. Indeed, when abundance is determined mainly by α_j, species who tolerate

252 CNDD will be more common (previously seen in Mangan *et al.* 2010; Chisholm &

253 Muller-Landau 2011; Mack & Bever 2014) – a result which matches some (but not all)

254 empirical studies.

255

256 We found that variation in CNDD also makes communities less stable by creating

257 competitive differences between species (i.e., mean fitness-differences, Fig. 2c). If seed

258 dispersal is limited, then some seeds will compete for sites held by their parent. If a

259 species is highly susceptible to CNDD (i.e., it has high α_j), then its non-dispersed seeds

260 have little chance of capturing such sites. Thus, species that can tolerate CNDD (i.e.,

261 have low α_j) have an advantage, because non-dispersed seeds are still decent competitors.

262 As a result, species with high α_j are likely to lose any site they hold each generation,

263 whereas species with low α_j can hold a site for multiple generations, giving the latter an

264 advantage. This mean fitness-difference effect is quantified for a species j as the amount

265 that ΔP_j differs from $\overline{\Delta P}$, (Chesson 2003):

$$\Delta P_j - \overline{\Delta P} \approx \left(\bar{\alpha} - \alpha_j\right)\left(\frac{d(1-d)S}{S-1} + \frac{d^2}{(S-1)^2}\right)$$

266

(5)

267 (Appendix: Analytical results). Though complex, this shows that a species' advantage is

268 proportional to the amount that its α_j is lower than the community average.

269

270 Thus, when species differ in their α_j, then species with a high α_j are at a disadvantage,

271 and the 'rare species advantage' is often weakened. As a result, the more CNDD varies

272 among species, the less likely they are to coexist (Fig. 2a) (previously seen in Miranda *et*

273 *al.* 2015). This holds for both deterministic (Fig. 2, S1) and stochastic (Fig. S2) systems.

274 If a species does not persist in a deterministic system, then it is quickly lost from a small

275 community (as expected, Nisbet & Gurney 1982). And, if stabilizing mechanisms are

276 weak or fitness differences are large, then species who are susceptible to CNDD have low

277 invader growth rates and low abundances, and are thus easily lost to demographic

278 stochasticity (Fig. S2).

279

280 Variation in CNDD is most harmful in communities where CNDD is weak (i.e., low $\bar{\alpha}$)

281 (previously seen in Miranda *et al.* 2015). In such communities, the stabilizing effect of

282 CNDD is already weak (eqn (4)), so they are less able to tolerate fitness-differences (Fig.

283 S1, S2).

284

285 Our model also shows that if seeds have limited dispersal (i.e., low *d*), then variation in

286 CNDD is more likely to lead to exclusion, rather than coexistence (Fig. 2). Reducing

287 dispersal increases mean fitness-differences (Fig. 2c, eqn (5)). If *d* is small, then many

288 seeds are exposed to CNDD, which increases the disadvantage of having a high α_j.

289 Reducing dispersal also weakens the stabilizing effect of CNDD (Fig. 2b, eqn (4)).

290 Simply, CNDD gives species an advantage when they become rare because they are less

291 likely to disperse near a conspecific. However, only seeds that disperse gain this

292 advantage, because non-dispersed seeds always experience CNDD generated by their

293 parent (Stump & Chesson 2015). Therefore, when *d* is low, rare species gain less of an

294 advantage than they would if *d* were high.

295

The negative effects of species-level differences in CNDD are caused by multispecies
interactions and limited seed dispersal. In a two-species community, the covariance term
in eqn (4) vanishes, and we are left with $\overline{\Delta P} \approx \frac{d^2\overline{\alpha}}{S-1}$ (Appendix: Analytical results). The
covariance represents the negative effect of a declining species being replaced by its
least-constrained competitors; this effect does not occur if a species has just one
competitor. Also, if there is 100% seed dispersal and $\alpha_j > 0$ for all species, then species
will always have positive invader growth rates (Appendix: Analytical results), and thus
will always coexist deterministically (previously shown in Chisholm & Muller-Landau
2011). Simply, if seeds always disperse away from their parent, then very rare species
will never experience CNDD, and thus always have an advantage over species who
experience some CNDD.

Does variation in CNDD differ from variation in other competitive factors?

Other factors can also produce competitive differences, such as if species have different
seedling recruitment rates. Thus, we examined if there is something special about
variation in CNDD that makes it different from other factors. We did this by comparing
communities that were structured by difference in susceptibility to CNDD, α_j, to those
where species differed in yield, Y_j. As shown previously (Stump & Chesson 2015), yield
produces no stabilizing effects, and contributes to species j's mean fitness-difference by

$$\Delta Y_j - \overline{\Delta Y} \approx \left(\ln Y_j - \overline{\ln Y}\right)\frac{d(2-d)S}{S-1}$$

(6)

where $\overline{\ln Y}$ is the mean of $\ln Y_k$ across all species (Appendix: Analytical results). Like
eqn (5), this term has a simple intuition: a species' advantage is proportional to the
amount that it is better than its average competitor. Thus, yield and CNDD susceptibility
can produce equivalent mean fitness-differences.

Communities where yield varies are more stable than communities where CNDD varies.
If all species have the same α_j, but vary in their yield, then the community-average
stabilizing mechanism is governed by eqn (3), which lacks the (generally negative)

324 covariance term. This occurs because when only Y_j varies, then all species are equally

325 regulated, but when α_j varies, then the most common species are often the least regulated.

326 Thus, for a given $\bar{\alpha}$, communities where yield varies can tolerate a wider range of mean

327 fitness-differences, compared to communities where CNDD varies.

328

329 We also tested how buffered each community is against demographic stochasticity. We

330 constructed several communities where α_j varies between species, and compared them to

331 communities where Y_j varies but invader growth rates are the same (the mean fitness-

332 differences and stabilizing mechanisms were therefore the same). Communities where

333 CNDD varies lost more species than communities where yield varies, and lost them faster

334 (Fig. 3). This difference occurred because of a difference in the relationship between

335 invader growth rate and abundance. Per-capita growth declines more quickly with

336 abundance for species with higher α_j (Chisholm & Muller-Landau 2011). Thus, for a

337 given invader growth rate, a species obtains a higher equilibrium abundance the lower its

338 α_j (Fig. 4). In communities where yield varies, every species has the same α_j, and

339 therefore abundance differences are similar to fitness-differences (Fig. 4b). In

340 communities where α_j varies, species with high α_j have low invader growth rates, and

341 therefore even lower abundances (Fig. 4a). The result is that communities where yield

342 varies tend to be more even than communities where CNDD varies (Fig. 3c). As a result,

343 weak competitors are rarer in communities where CNDD varies, and thus more likely to

344 be lost due to demographic stochasticity.

345

346 The difference between CNDD and yield also appear to be due to dispersal limitation and

347 multi-species interactions. In a two-species community with d=1, communities where

348 CNDD varies are nearly identical to those where yield varies (Fig. S3).

349

350 ***The model's suggestions for how to estimate the impact of CNDD***

351 Though our model is simple, it offers two ways of estimating how variation in CNDD

352 affects coexistence in real communities. First, we can examine how variation in α_j alters

353 its average effect across all species (i.e., how it impacts the stabilizing mechanism, $\overline{\Delta P}$).

354 We can do this by dividing eqn (4) by (3),

$$\frac{\overline{\Delta P}_{\text{with variation in CNDD}}}{\overline{\Delta P}_{\text{no variation in CNDD}}} \approx \frac{\dfrac{\bar{\alpha}}{S-1} + \text{cov}(\alpha_j, N_j)}{\dfrac{\bar{\alpha}}{S-1}}.$$

(7)

If common species are less susceptible to CNDD, then this ratio will be less than 1, which suggests that variation in α_j weakens its stabilizing effect.

Second, insights can be gained by estimating how CNDD affects the invader growth rates of individual species (Barabás *et al.* 2018). We do this by adding the stabilizing effect of CNDD (eqn (4)) to its mean fitness-difference effect on species j (eqn (5)),

$$\Delta P_j \approx (\bar{\alpha} - \alpha_j)\left(\frac{d(1-d)S}{S-1} + \frac{d^2}{(S-1)^2}\right) + d^2\left(\frac{\bar{\alpha}}{S-1} + \text{cov}(\alpha_r, N_r)\right).$$

(8)

If ΔP_j is negative, it means that CNDD makes species j less able to persist (compared to a CNDD-free community). A negative ΔP_j thus suggests that species j will go extinct in the absence of equalizing trade-offs or other stabilizing mechanisms. Additionally, examining the distribution of ΔP_j values for all species in the community can show whether CNDD is strongly stabilizing (i.e., $\Delta P_j > 0$ for all species), or if it mainly produces mean fitness-differences (i.e., $\Delta P_j < 0$ for about half of species, and the effects are near zeros-sum).

How does CNDD affect coexistence in a real-world tropical tree community?

Data from the tree community on BCI suggests that variation in CNDD weakens its stabilizing effect. Using basal area to parameterize frequency, eqn (7) suggests that variation in CNDD reduces its stabilizing effect by 42% (Fig. 5a). Using the number of adults to parameterize frequency, eqn (7) suggests that variation in CNDD reduces its stabilizing effect by only 6% (Fig. 5a). This difference is driven by the most common species: three of the four species with the most basal area experience weak CNDD, but only one of the five species with the most adults experiences weak CNDD (Fig. 5a).

Eqn (8) suggests that unless d is nearly 1, CNDD will create large fitness-differences, and thus a wide distribution of ΔP_j values (Fig. 5c). However, the stabilizing effect of CNDD

382 is inversely proportional to species richness, and will therefore be weak. This suggests

383 that unless *d* is nearly 1, then the fitness effects of CNDD will outweigh its stabilizing

384 effect (Fig. 5b), and thus that CNDD is making many species less likely to persist, rather

385 than strongly maintaining diversity.

386

387 **<u>Discussion</u>**

388 In many plant communities, common species are less susceptible to CNDD than rarer

389 species (Klironomos 2002; Petermann *et al.* 2008; Comita *et al.* 2010; Mangan *et al.*

390 2010; Kobe & Vriesendorp 2011), but the long-term implications of this pattern have not

391 previously been fully explored. Here we show that if common species are less susceptible

392 to CNDD, then the community is less stable. Communities are most stable when every

393 species suffers from uniformly high CNDD, because rare species suffer less mortality

394 than common ones. If a few species suffer higher CNDD, the main effect is that those

395 species will be weaker competitors. Additionally, if a few species are immune to CNDD,

396 then the community will usually become dominated by those species, weakening the

397 mechanism overall.

398

399 Our results indicate that seed dispersal affects whether CNDD promotes or undermines

400 coexistence. Models suggest that if each species gains an advantage in "away" sites (i.e.,

401 ones far from conspecifics), then rare species have an advantage because they have more

402 away sites (Bever 2003). This argument implicitly assumes that seeds of rare species can

403 get to those away sites; if dispersal is low, this will often not be the case. Our model

404 agrees with previous work showing that low dispersal weakens the stabilizing effect of

405 CNDD, because rare species cannot take full advantage of away sites (Murrell 2010;

406 Stump & Chesson 2015). We also make the novel claim that low dispersal increases

407 mean fitness-differences, putting species that are susceptible to CNDD at a disadvantage

408 overall. In our model, this occurred because high α_j reduced the ability of a non-dispersed

409 seedling to capture its parent's site. However, we expect a similar effect in models with

410 more realistic dispersal: if many seeds cannot escape the CNDD generated by their

411 parent, then species with low α_j should have an advantage over species with high α_j.

412

413   Previous studies have shown that at small scales, diversity increases during the seed-to-

414   seedling transition (Harms *et al.* 2000). That local-scale observation can be consistent

415   with decreasing diversity at the landscape scale. At any given site, the most abundant

416   seeds will be those who came from nearby trees. Such seeds will therefore experience

417   CNDD, and negative frequency-dependent survival will be occurring at the local level.

418   However, competitive differences appear at the larger scale, because some species lose

419   most of their non-dispersed seeds, whereas others do not. Integrated over a landscape,

420   such differential mortality can lead to exclusion (Fig. 2a). Thus, CNDD can boost

421   diversity at the local neighborhood scale, but reduce diversity at the landscape scale.

422

423   Our finding that variation in CNDD makes species less likely to coexist is consistent with

424   results from Miranda et al. (2015). Their model showed that variation in susceptibility to

425   CNDD leads to competitive exclusion and reduced (Shannon) diversity at the

426   community-level, especially when the mean effect of CNDD is weak. Our model

427   expands on this result by showing how CNDD interacts with dispersal, how differences

428   in CNDD compare with differences in other competitive factors, and how CNDD

429   produces stabilizing mechanisms and mean fitness-differences.

430

431   Our model shows that sensitivity to CNDD can cause a species to be rare (in agreement

432   with Mangan *et al.* 2010; Chisholm & Muller-Landau 2011; Mack & Bever 2014;

433   Miranda *et al.* 2015), and that such rarity can make species prone to extinction (in

434   agreement with Nisbet & Gurney 1982). However, many factors can cause species to be

435   rare, including if they are weak competitors that are hindered by interspecific

436   competition. Previous work has shown that a species who is rare because of strong self-

437   limitation (negative frequency dependence) is less likely to go extinct than a species who

438   is rare because it is suppressed by competitors (Yenni *et al.* 2012). Thus, a better

439   understanding of what drives rarity in ecological communities will help us understand

440   how species coexist.

441

442   Our model makes several simplifying assumptions. It assumes species interact with all

443   heterospecifics similarly, which they do not (Morris *et al.* 2007; Liu *et al.* 2012; Wills *et*

444   *al.* 2016). Thus, our model likely overestimates the stabilizing effect of CNDD, but also

445   likely overestimates the mean fitness-differences it produces (Stump 2017). Our model

446   assumes that α_j is fixed, though it may vary in space (Inman-Narahari *et al.* 2016;

447   Krishnadas & Comita 2018), time (Janzen 1972; Feer & Forget 2002), or with population

448   size (Marden *et al.* 2017). It is not clear how relaxing this assumption would change the

449   model's behavior, though we expect our main results to hold (i.e., between-species

450   difference in α_j undermine coexistence). Our model assumes that seeds are either

451   dispersed or not dispersed. Preliminary calculations suggest that using more realistic

452   dispersal kernels has an effect that is similar to increasing *d*. Finally, we assume that *d* is

453   the same for all species, which is not true (Clark *et al.* 2005). Preliminary calculations

454   and intuition suggest that species with high dispersal will have an advantage over species

455   with low dispersal. Each of these effects should be examined in future models.

456

457   With those caveats, our model suggests that CNDD has a mostly negative effect on BCI's

458   tree diversity, because it produces a small stabilizing effect and large mean fitness-

459   differences (Fig. 5). It is possible that CNDD was estimated incorrectly (Freckleton *et al.*

460   2006), or that the measurement of CNDD by Comita et al. (2010) was not appropriate for

461   parameterizing our model. However, if our results do reflect reality, then at least one of

462   three things is happening. First, many species may be going extinct, and competitive

463   exclusion is simply slow. In this case, diversity could be slowly declining, or it could be

464   maintained by an immigration/speciation-extinction balance (Hubbell 2001). Second,

465   other stabilizing mechanisms, such as habitat partitioning (Johnson *et al.* 2017) or the

466   temporal storage effect (Usinowicz *et al.* 2012), may be offsetting any fitness-differences.

467   Third, the fitness-differences may be offset by an equalizing trade-off. For example,

468   studies have suggested that fast-growing species suffer higher CNDD than slow-growing

469   species (Kobe & Vriesendorp 2011; Zhu *et al.* 2018). This suggests a competition-

470   predation trade-off, where species that are more susceptible to CNDD are stronger

471   competitors in the absence of CNDD (i.e., species with high α_j also have high Y_j). In this

472   case, CNDD could promote coexistence both by producing a stabilizing effect and by

473   offsetting other mean fitness-differences.

474

475 We suspect that our BCI results are not uncommon. The stabilizing effect of CNDD is

476 inversely proportional to species richness (eqn (4)). This occurs because an increase in

477 species richness decreases the frequency of each species. If every species has low

478 frequency, then few seeds will encounter conspecifics; as a result, CNDD will hardly

479 reduce survival, even for species at equilibrium. If a species at equilibrium is hardly

480 constrained by CNDD, then there will be little benefit to being rare. This is a common

481 result for models of diffuse competition: any 'rare species advantage' will be weak if

482 every species is rare (Chesson 2000; Stump 2017). However, mean fitness-differences do

483 not typically change with diversity (eqn (5)): a tree that experiences 10% more mortality

484 than all of its competitors is at a disadvantage, whether it is competing against two

485 species or 200. Thus, we predict that in diverse communities, the fitness effects of CNDD

486 will usually outweigh its stabilizing effect when dispersal and CNDD are both localized.

487

488 In conclusion, our model suggests that while CNDD promotes coexistence, interspecific

489 variation in CNDD undermines coexistence, especially when seed dispersal is low. The

490 net effect is that CNDD can actually lead to competitive exclusion. Future tests of the

491 Janzen-Connell hypothesis should determine not only if CNDD is occurring, but how

492 much it varies between species, how it covaries with abundance, and the spatial scale of

493 dispersal and CNDD.

494

502

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636

637 **Table 1.** Parameters and variables use in the model.

Parameter	Description
α_j	Species j's susceptibility to CNDD
$\bar{\alpha}_j$	Mean of α_j across all species
Y_j	Species j's yield (i.e., generalized competitive ability)
δ	Adult death rate
d	Fraction of seeds dispersed
S	Number of species
Variable	**Description**
N_j	Frequency of species j adults across the landscape
C_j	Competition-weighted number of seeds at a site held by species j (after CNDD)
$\tilde{\lambda}_j$	Expected finite rate of increase (i.e., discrete-time growth rate) of species j
ΔP_j	The amount that species j's invader growth rate is affected by CNDD
ΔY_j	The amount that species j's invader growth rate is affected by yield

638

639

(a) Seeds are produced and dispersed.
(b) Seeds die from CNDD.
(c) Adults die.
(d) Lottery competition to capture gaps.

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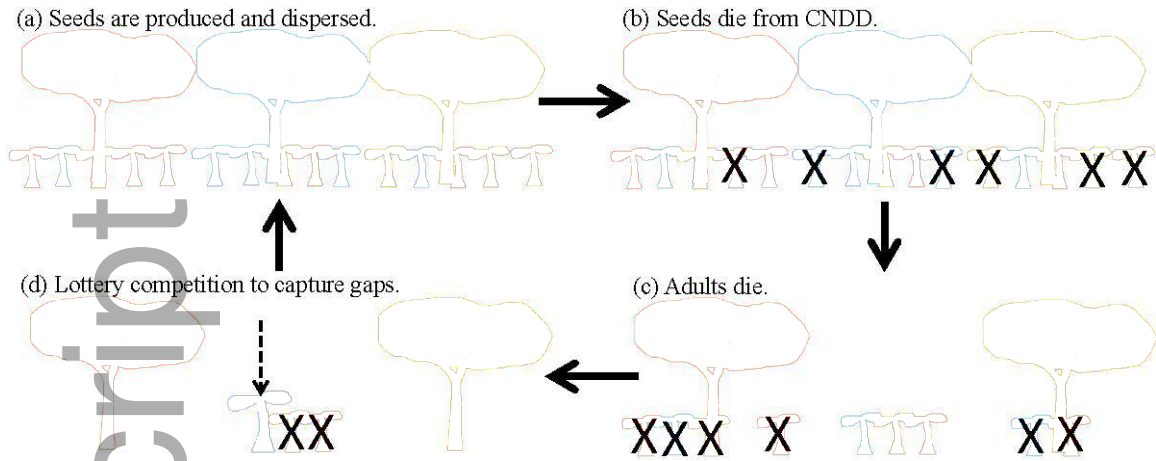
641 **Figure 1** Model outline. We modeled competition for light gaps using a four-step

642 approximation of the life cycle of a tree. (a) First, each adult makes Y_j seeds. $Y_j d$ seeds

643 stay in the parent's site, and the other $Y_j(1–d)$ seeds disperse uniformly around the

644 community. (b) Second, seedlings die from CNDD. A seedling under a conspecific tree

645 dies with probability α_j; the rest always survive. (c) Third, adults die with probability δ. If

646 an adult survives, the seedlings underneath it die. (d) Last, one seedling in each tree-fall

647 gap is randomly chosen to become an adult by the next time step.

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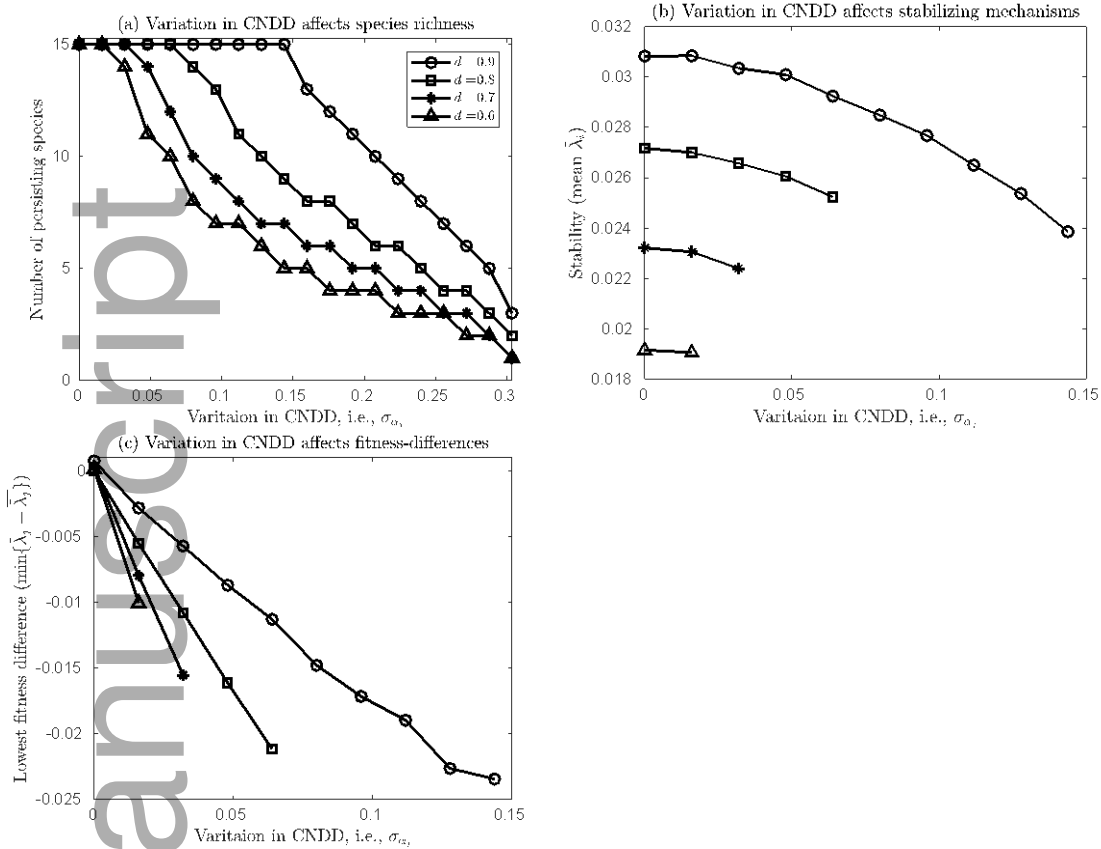
651 **Figure 2** Variation in CNDD reduces diversity. We generated communities of 15 species
652 that varied in their susceptibility to CNDD, α_j. We considered communities where all
653 species had the same α_j (i.e., where $\sigma_\alpha = 0$), up to communities where α_j was nearly 0 for
654 one species. We assumed that $\bar{\alpha} = 0.5$ in all communities. (a) We determined how many
655 species coexist for various levels of seed dispersal, d. Deterministic coexistence was
656 determined using computer simulations (Appendix: Computer simulations). (b) We
657 quantified the mean invader growth rate (i.e., the stabilizing effect of CNDD) in each
658 community, $\overline{\Delta P}$. The lines are drawn until the first species went extinct. (c) We quantified
659 the mean fitness-difference (i.e., $\Delta P_j - \overline{\Delta P}$) between weakest competitor and the rest of
660 the community. The lines are drawn until that species went extinct. Parameters: $Y_j = 1$, δ
661 $= 0.4$, α_j varied uniformly; for example, when $\sigma_\alpha = 0.3035$, α_j varied from 0.025 to 0.975.

662

(a) How fast species are lost in each community

(b) Number of species maintained in each community

(c) Community evenness

663

664
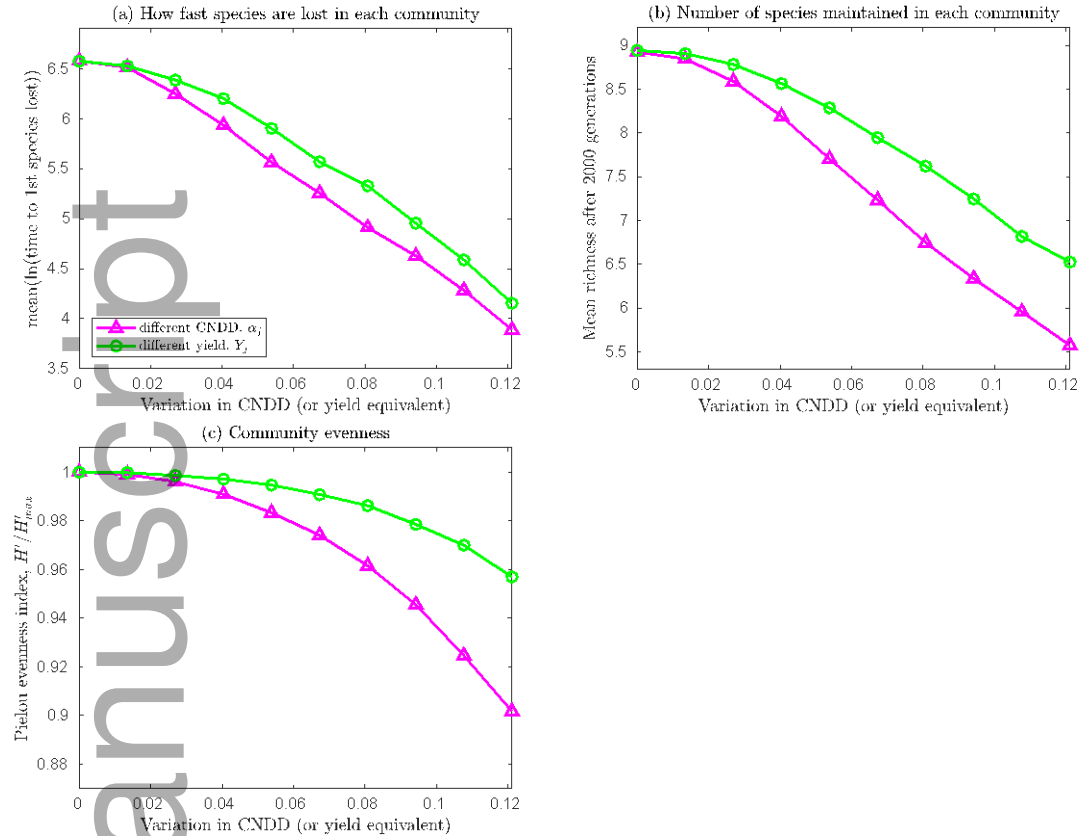
Figure 3 Communities structured by differences in CNDD are less stable against demographic stochasticity compared to communities structured by differences in yield. We generated a series of communities in which species differed in susceptibility to CNDD, α_j. These communities contained 10 species that would coexist in a deterministic model. We then created an equivalent set of communities where species differed in yield, Y_j, but invader growth rates were approximately the same (Appendix: Computer simulations). Species then competed in a small community (2000 sites) for 2000 generations. (a) Communities where CNDD varied tended to lose species faster than those where yield varied. (b) Communities where CNDD varied tended to have fewer species after 2000 generations. (c) The difference in stability occurs in part because when α_j varies, communities are less even than when Y_j varies. As a result, rare species are rarer –and thus more prone to demographic stochasticity– when α_j varies. Parameters: $d =$ 0.9 and $\delta = 0.4$. In communities where α_j varied, $Y_j =1$ and $\bar{\alpha} = 0.4$.

678

(a) Abundance vs. growth, α_j varies

(b) Abundance vs. growth, Y_j varies

679
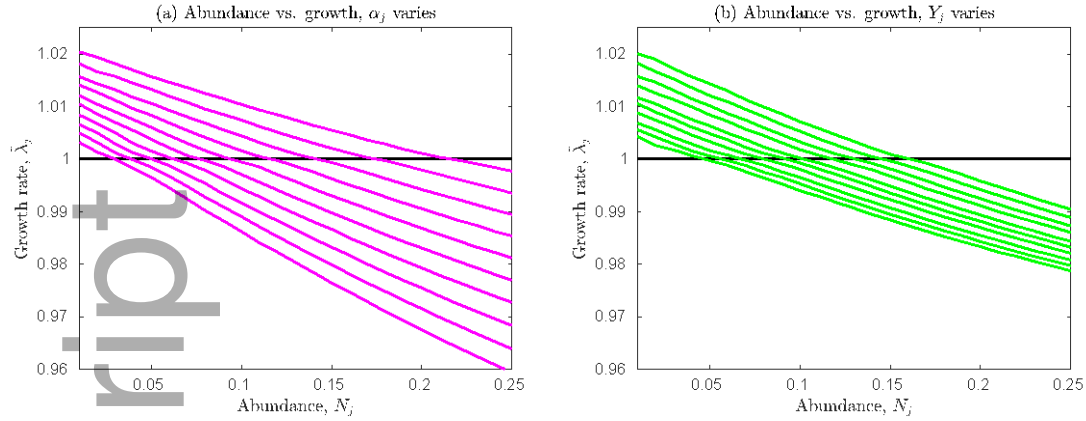
680 **Figure 4** Why variation in CNDD makes communities less even than variation in yield.

681 Here we show the relationship between frequency, N_j, and per-capita growth, $\tilde{\lambda}_j$, for

682 species in two analogous communities ($\sigma_\alpha = 0.094$ and yield equivalent from Fig. 3).

683 Each colored line represents a different species. (a) When CNDD (α_j) varies, the

684 relationship between N_j and $\tilde{\lambda}_j$ is more negative for species with a high α_j. (b) When

685 yield (Y_j) varies, but every species has the same α_j, then the relationship between N_j and

686 $\tilde{\lambda}_j$ nearly the same for all species. As a result, the community is more even at equilibrium

687 in community (b) than in community (a).

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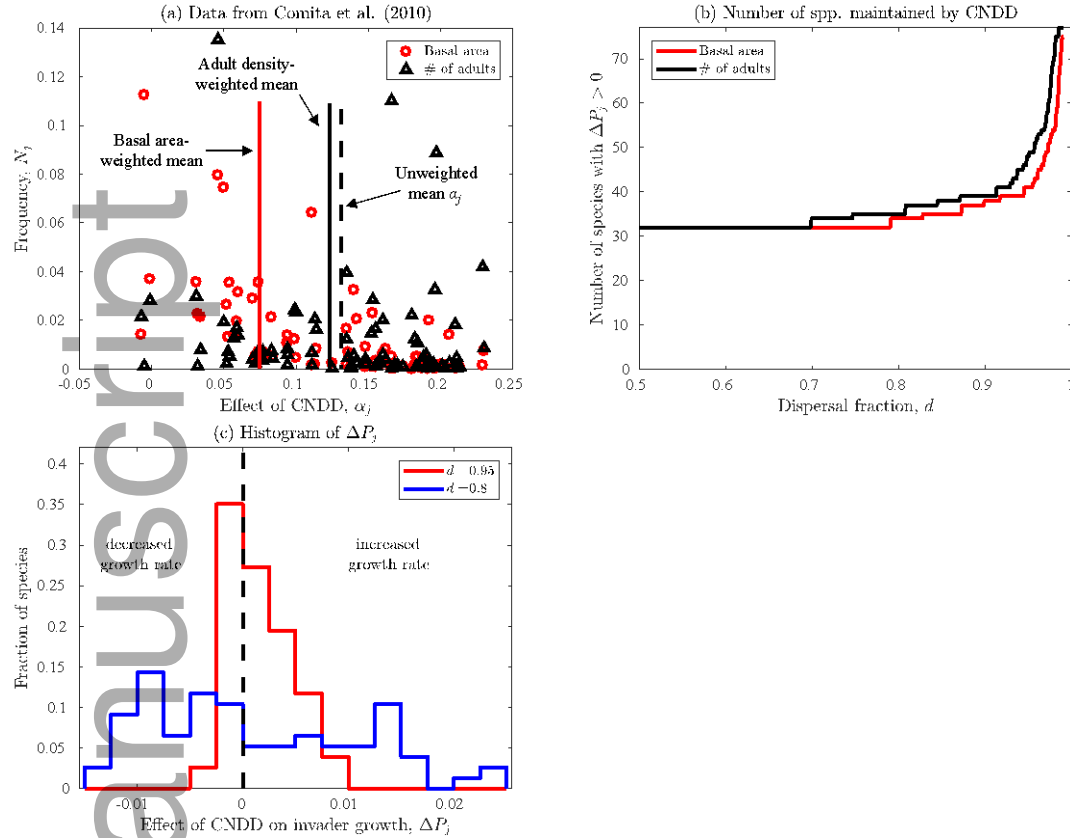
Figure 5 The net impact of CNDD on tropical trees of Barro Colorado Island. (a) Here
we show abundance and CNDD data from Comita *et al.* (2010), who measured how
conspecific adult density affected seedling survival. We display data for 77 species of
canopy trees, using both basal area and number of reproductive adults as possible
measures of abundance. In both cases, the abundance-weighted mean α_j (the solid lines)
was lower than the unweighted mean of α_j (the dotted line), which should reduce the
stabilizing effect of CNDD. (b) We used eqn (8) to test how many species had their
invader growth rates boosted by CNDD (i.e., had $\Delta P_j > 0$), for a range of dispersal values.
If ΔP_j is negative for a given species, it suggests that CNDD is contributing more to
exclusion than persistence for that species. (c) A histogram of two sets of ΔP_j values,
using number of reproductive adults as measures of density.

(a) Variation in CNDD affects species richness

(b) Variation in CNDD affects stabilizing mechanisms

(c) Variation in CNDD affects fitness-differences
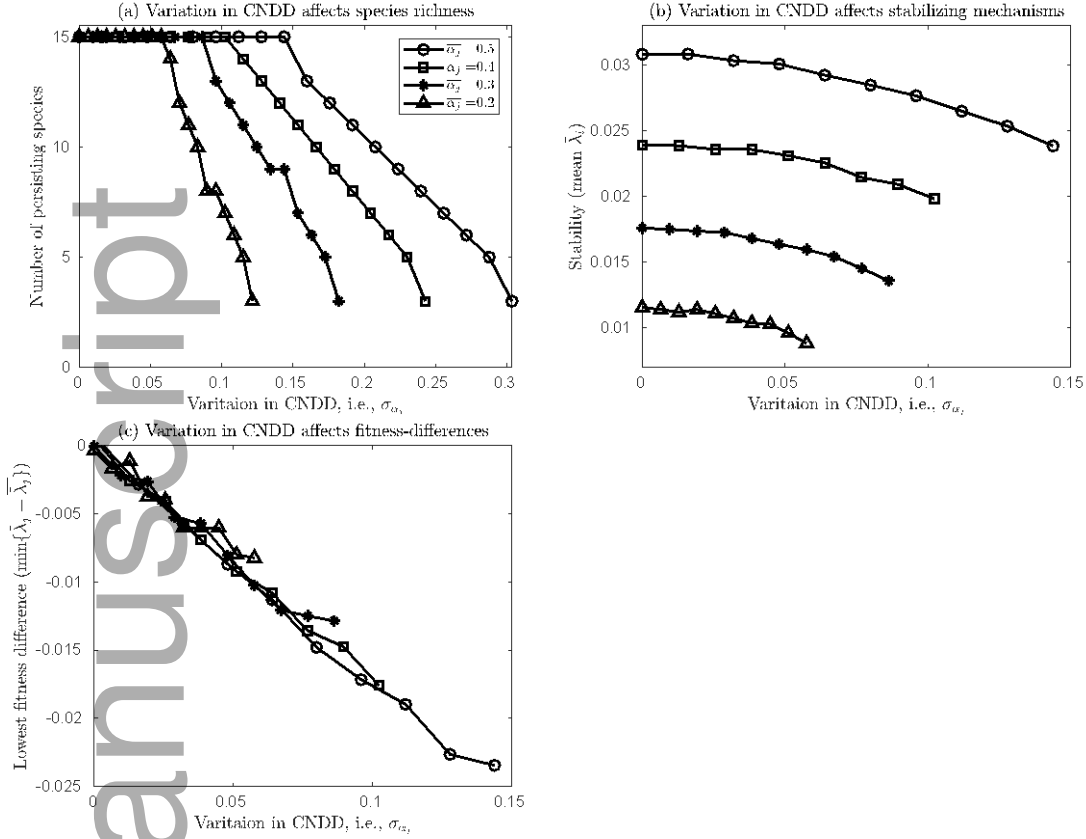
Figure S1 Communities are more stable when mean CNDD is high. We generated several communities in a manner similar to those in Fig. 2; however, instead of varying dispersal, we varied the average impact of CNDD, $\bar{\alpha}$. (a) Fewer species coexisted when CNDD varied, and this effect was strongest when $\bar{\alpha}$ was low. (b) Mean invader growth rates (i.e., stabilizing mechanisms) were weakened when CNDD varied, especially when $\bar{\alpha}$ was low. (c) Variation in CNDD produced fitness differences. Parameters: d=0.6, δ=0.4, Y_j=1, α_j varied uniformly.

(a) How fast species are lost in each community

(b) Number of species maintained in each community
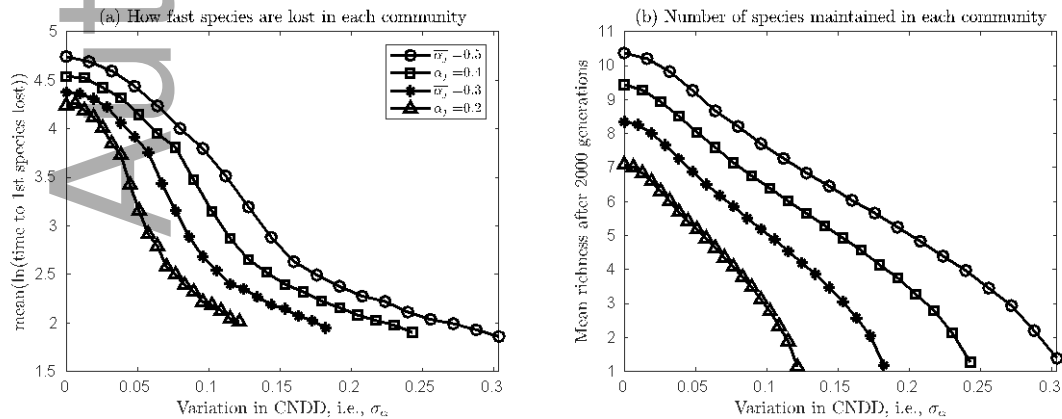
714   **Figure S2** Variation in CNDD reduced community robustness to CNDD. We allowed the

715   communities in Fig. S1 to compete in a small forest (2000 sites) for 2000 generations.

716   Each species began close to equilibrium density, to a minimum of 1% of sites. We

717   replicated each community 5000 times. (a) Here we show the mean ln{time to first

718   species loss}. (b) Here we show the mean number of species remaining after 2000

719   generations.

720

(a) Determinstic stability

(b) How fast species are lost in each community

- different CNDD, low α_j
- different yield, high Y_j
- different CNDD, high α_j
- different yield, low Y_j
- mean, variable α_j
- mean, variable Y_j

721

(c) Number of species maintained in each community

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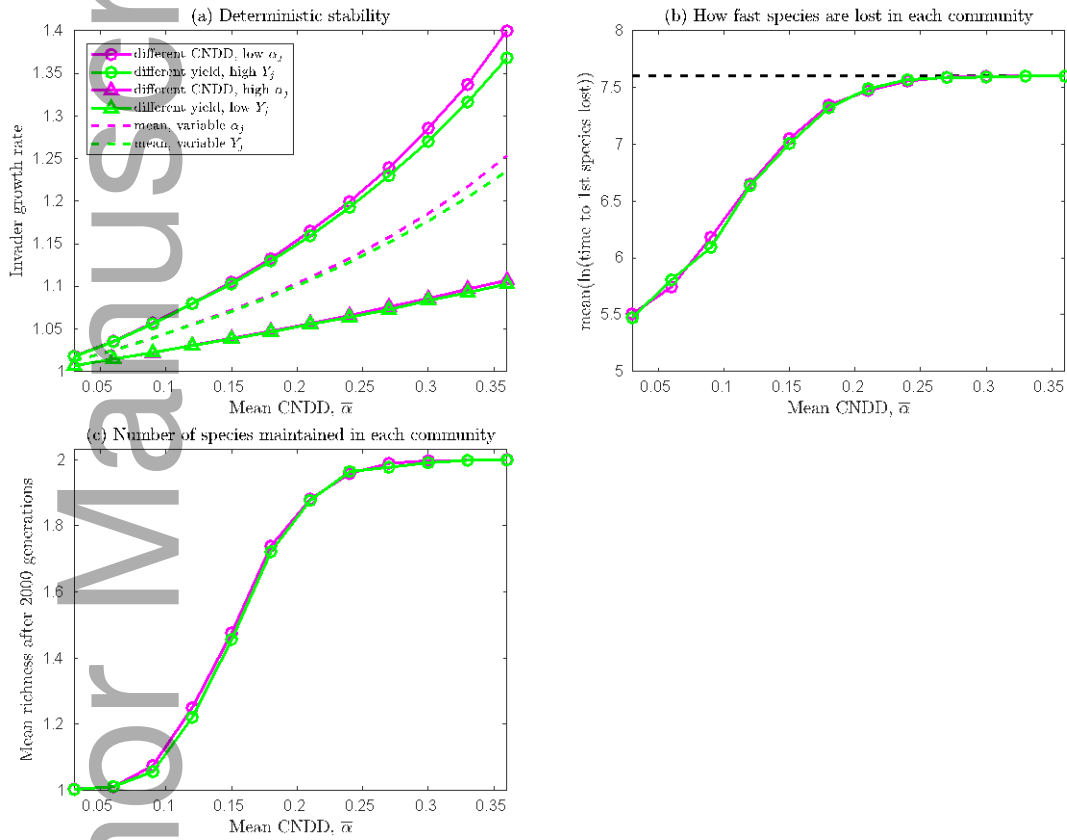
723   **Figure S3** Effect of CNDD vs. yield in a two-species community without dispersal

724   limitation. We examined communities where α_j differed between species, and

725   communities where Y_j differed between species. We set our parameters so that $\bar{\alpha}$ could

726   vary, but the rare species always obtained 30% of sites at equilibrium. (a) Here we show

727   the invader growth rates of each species, and their mean. (b) We allowed species to

728   compete for 2000 generations in a community with 300 adults. Here we show the mean

729   ln{time to first species loss}. It was set to ln{2000} if neither species went extinct

730   (shown as the dotted line). (c) Here we show the mean number of species that survived

731   for 2000 generations. Parameters: d=1, δ=0.4; $\bar{\alpha}$ varied from 0.03 to 0.36.

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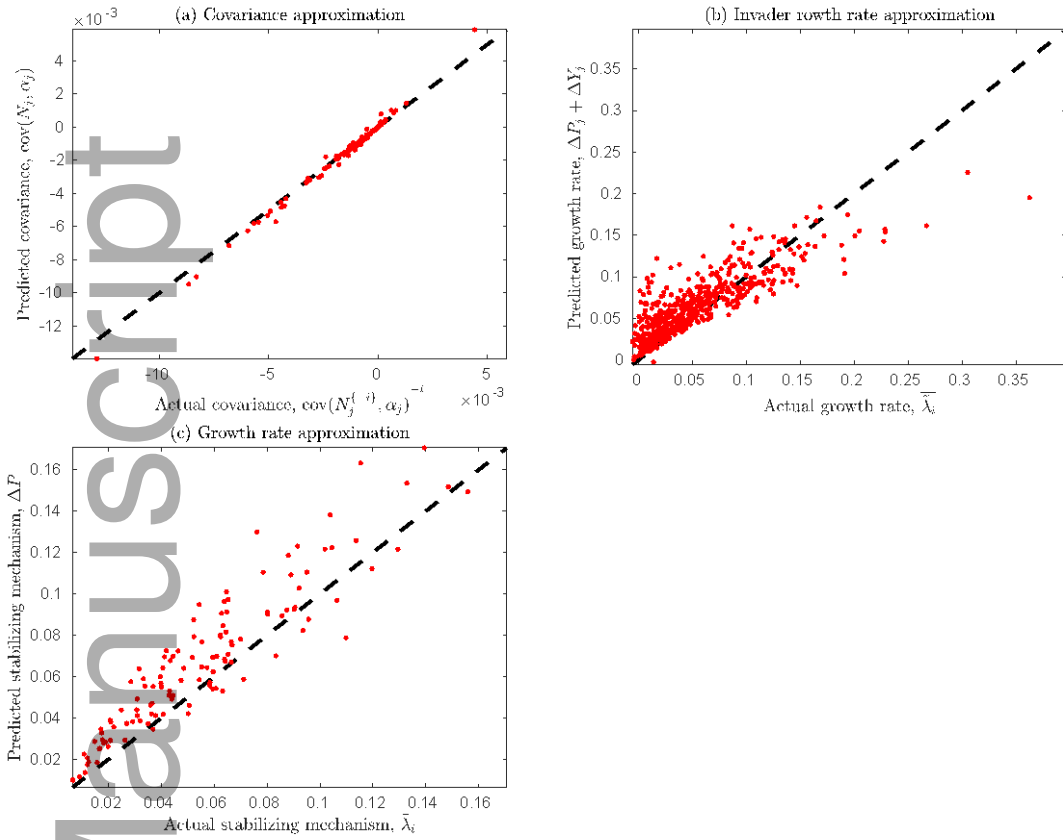
Figure S4 Testing our approximations. We generated 200 random communities, as described in Appendix: Computer simulations. We discarded any community that contained 2 or fewer coexisting species, and were left with 157 communities. (a) We tested our approximation $\mathrm{cov}(\alpha_r, N_r) \approx \overline{\mathrm{cov}(\alpha_r, N_r)}^{-i}$. Each red dot represents these values in a particular community. If this approximation were exact, every dot would be on the one-to-one line. (b) We tested our approximations for the invader growth rate, which could be calculated as $\Delta P_j + \Delta Y_j$. Each dot represents a single individual in one of our communities. (c) We tested our approximation for the community-average stabilizing mechanism, $\overline{\Delta P}$. Each dot represents the value for a particular community.

Appendix: Computer simulations

We simulated our community using code that was modified from Stump & Chesson (2015) and Stump (2017). The community is made up of X sites, each of which contains 1 adult. To calculate growth rates or equilibrium densities, X was typically set at 50,000; to calculate the effect of demographic stochasticity, X was typically set to 2000. The community is initiated at either the equilibrium density or at equal densities for each species. During each time step, each adult dies with probability δ. If the adult dies, then one seed is randomly chosen to replace it. If a site was previously held by species j, then there are $Y_j(1 - d + N_jd)(1 - \alpha_j)$ seeds of species j at that site; otherwise there are Y_jN_jd seeds of species j there.

To calculate invader growth rates, we selected one species to be an invader, and the rest were called the "residents" (i.e., the species at equilibrium). The invader's density was held at between 0.1% and 0.5% of community biomass. If the invader's density rose above 0.5%, then some of the invaders were killed and replaced by random residents (weighted by density). If the invader's density shrank below 0.1%, then a few residents were killed and replaced by the invader. After a burn-in period (typically 500 to 1000 time steps), we recorded the invader's growth rate at each time step. The growth rate ($\tilde{\lambda}_j$) was recorded as the number of adult invaders at the end of the time step (before adjustment), divided by the number at the start of the time step. This was averaged over typically 1000 time steps, and averaged across multiple simulation runs.

To calculate the growth rate as a function of abundance (Fig. 4), we followed a similar procedure as the invader growth rate, except that the abundance was held at much higher level (between 0.1% of community biomass and 25% of community biomass).

To calculate equilibrium abundance, we simulated community dynamics in a large community for a long period of time, and calculated the mean of N_j across many time steps (after a burn-in period).

For Fig. 3, we needed to make pairs of communities with equal fitness-differences, but where one community had interspecific variation in α_j, and the other had variation in Y_j. To do this, we first simulated the dynamics in a community where α_j differed between species, but yields were the same. This gave us the normalized invader growth rate, $\tilde{\lambda}'_j$, of each species (we define $\tilde{\lambda}'_j = (\tilde{\lambda}_j - 1)/\delta$)). We used this to construct the community where Y_j varied. We set α_j in the second community to (S–1) times the mean invader growth rate ($\bar{\tilde{\lambda}'_l}$) in the first community. We assumed that the mean yield across all species would be 1. Then, we set Y_j for each species as

$$Y_j = \exp\left\{\left(\tilde{\lambda}'_j - \bar{\tilde{\lambda}'_l}\right)\frac{S - 1}{2Sd(1 - d)^2}\right\}.$$

(A.1)

Simulations suggest that this comes very close to giving each species the same invader growth rate.

Testing our analytical results

In the next section, we derive an analytical approximation for the invader growth rate. To test whether our approximations accurately predicted the growth rate, we generated 200 random communities. Parameters were chosen randomly (described below). Each community was seeded with between 3 and 11 species. We simulated community dynamics for 6000 time steps (2400

generations with δ=0.4), and eliminated any species whose frequency declined below 0.001. We calculated cov(N_j, α_j) in this community. If at least three species remained, then we then calculated the invader growth rate for each member of the community. We ran simulations for 6000 time steps, and averaged the invader growth rate over the final 2000 time steps, in a community of 100,000 adults. We calculated cov(N_r, α_r) in each invasion community, and the mean stabilizing mechanism (i.e., $\tilde{\lambda}'_j$ averaged across species), along with our analytical predictions for each growth rate (i.e., $\Delta P_j + \Delta Y_j$).

Here we describe our parameters. We write U(X,Y) to mean a uniform random number between X and Y. We selected the initial number of species as a uniform integer between 3 to 11. We selected the dispersal rate as d =U(0.65, 1). We selected the amount that yields would vary in the community as Y_{diff}=U(0,0.2), and set each species' yield as $Y_j = 1+$U(0,Y_{diff}). We parameterized yield with two different random variables in order to produce communities with different levels of yield variation. We chose the community average effect of CNDD as $\bar{\alpha}$ = U(0.05, 0.55), the amount that α_j could vary as α_{diff}=U(0, 0.5), and the value of each species sensitivity to CNDD as α_j = min(1, $\bar{\alpha}$(1+U($-\alpha_{\text{diff}}$/2, α_{diff}/2))). Similar to yield, we parameterized α_j with three parameters so that communities could have different mean effects of CNDD, and different levels of variation in CNDD.

We feel our approximations work very well (Fig. S4). As we explain below, the value cov(N_j, α_j) in eqn (4) is an approximation, but it fits the data extremely well (Fig. S4a). Simulations suggest that our approximation slightly overestimates the growth rates of species with $\tilde{\lambda}'_j$<0.05, and underestimates the growth rates of species with $\tilde{\lambda}'_j$>0.15 (Fig. S4b); however, the fit in general is good (r^2=0.74). Thus, we expect that our model produces an additional mean fitness-difference that our approximation does not account for. Finally, our results suggest that we overestimate the stabilizing mechanisms slightly (Fig. S4c), but that overall the fit is extremely good (r^2=0.85). Thus, we feel confident in our approximation.

Appendix: Analytical results
In this section, we first derive the formula for the finite rate of increase of a species, eqns (1) and (2) of the main text. We then derive the formulas for the stabilizing and fitness-difference terms, eqns (3) through (6) of the main text. Our methods are based loosely on previous work by Chesson (2000a) and Stump & Chesson (2015). To derive eqns (3) through (6), we first use Taylor series to approximate the seed recruitment; we then use this approximation simplify the equation for $\tilde{\lambda}'_j$; we then partition an invader's growth rate into terms caused by CNDD (ΔP_j) and those caused by yield (ΔY_j); finally, we calculate the stabilizing mechanisms and mean fitness differences in this model.

Our methods use Taylor series, and thus require a small-effect approximation. Basically, we require that each α_j is small enough and the Y_j's are similar enough that we can approximate the chance of recruitment as a linear function of the α_j and Y_j values. Technically, this means that every α_j term is O(α) for a small α, and that $Y_j/Y_k = 1+$O(α) for any j and k. As we show, if this assumption holds, then the invader growth rate will be approximately $1+$O(α), and terms that are O(α^2) or smaller can be safely ignored. Simulations suggest that our approximations will be correct, even if α is extremely large (e.g., if it varies between 0.1 and 0.8 in a 10-species

community). Below we write "≈" if two terms are the same up to order α, i.e., $X \approx Y$ iff $X = Y + O(\alpha^2)$.

Deriving the finite rate of increase

We first derive eqn (1), which gives the number of seeds dispersed to a site held by an adult of species j, weighted by yield and CNDD,

$$C_j = Y_j\big(1 - d + dN_j\big)\big(1 - \alpha_j\big) + \sum_{k \neq j} Y_k dN_k \,.$$

(A.2)

First, the species j adult which occupies that site will produce Y_j seeds, and a fraction $(1 - d)$ of those seeds will stay at the site. However, a fraction α_j of those seeds will die from CNDD. Thus, the adult at a site will contribute $Y_j(1 - d)(1 - \alpha_j)$ seeds to that site. Next, each adult of species k will produce Y_k seeds, and disperse a fraction d of them uniformly around the environment. If there are X sites in the community, then each adult will send $Y_k d/X$ seeds to every site (this step makes two implicit assumptions, see below). Because N_k is the fraction of sites held by species k, there are XN_k individual adults. Thus, $XN_k(Y_k d/X) = Y_k dN_k$ seeds are dispersed to each site; this makes up the term after the summation. Finally, seeds of species j who disperse to this site have a probability α_j of dying from CNDD; thus, there will be $Y_j dN_j(1 - \alpha_j)$ seeds of species j at a site due to dispersal. Summing these, we have our equation for C_j.

We make two assumptions about dispersed seeds. First, we assume that a seed can be "dispersed" to its parent's site. This is mathematically equivalent to assuming that all "dispersed" seeds leave their parent's site and increasing the fraction of non-dispersed seeds to $(1 - d + d(X+1)/X)$. This effect will be trivial for large X. Second, we assume that there are an infinite number of seeds, so that every site receives exactly $Y_k dN_k$ seeds of species k (no matter how small N_k is). We did this for mathematical convenience. Preliminary simulations suggest that the results would be the same if we tracked every individual site, and the number of seeds arriving at a site was a Poisson random variable with mean $Y_k dN_k$. Indeed, this basic approach was taken by Muller-Landau (2010), who found that stochastic seed arrival would not affect results as long as seed production was large enough. Stochastic seed arrival may be worth examining, but was beyond the scope of this particular study.

We next derive eqn (2), the growth rate of a population. In our model, every individual within a species will have the same expected fitness: there is no extrinsic variation in the environment (e.g., habitat), seed dispersal is uniform, and all dynamics take place within a site. Thus, our equation for the finite rate of increase, $\tilde{\lambda}_j$, can be derived by determining the expected survival and reproduction of an individual. Eq (2) is

$$\tilde{\lambda}_j = (1 - \delta) + \frac{\delta Y_j(1 - d)(1 - \alpha_j)}{C_j} + \delta Y_j d\left(\frac{N_j(1 - \alpha_j)}{C_j} + \sum_{k \neq j} \frac{N_k}{C_k}\right).$$

(A.3)

Each adult survives with probability $(1 - \delta)$; this is the first term in (2). Each adult of species j produces $Y_j(1 - d)$ seeds that do not disperse, but a fraction α_j of those seeds will be killed by CNDD. Thus if an adult dies (which occurs with probability δ), then one of the C_j seeds at the site will become the adult (chosen randomly). Thus, the probability that a tree dies and then one

of its offspring captures its site is $\delta Y_j(1 - d)(1 - \alpha_j)/C_j$; this gives the second term. Finally, an adult will produce $Y_j d$ seeds that are dispersed around the community. It will disperse $Y_j d/X$ of those seeds to each individual site (see caveats in the previous paragraph). A seed that disperses to site occupied by a species k adult will recruit to that site if the adult dies (which occurs with probability δ) and it wins lottery competition (which occurs with probability $1/C_k$). Thus, the offspring of an adult at site y will capture a heterospecific site x with probability $\delta Y_j d/X C_k$. There are $X N_k$ sites held by species k adults. Thus, a given adult is expected to capture $\delta Y_j d N_k/C_k$ sites held by heterospecific species k; this is the number after the summation. Finally, if a seed disperses to a conspecific site, then similar logic holds, except that the seed's probability of capturing the site is reduced by α_j. Thus, a given adult is expected to capture $\delta Y_j d N_j(1 - \alpha_j)/C_j$ conspecific site with dispersed seeds. Together, this is eqn (2).

To calculate stabilizing mechanisms and mean fitness-differences, one must weight the invader growth rates by the sensitivity to competition (Chesson 2003). For lottery models, this sensitivity to competition is the death rate, δ (Chesson 2003; Stump & Chesson 2015). Thus, for notational simplicity, we define $\tilde{\lambda}'_j = (\tilde{\lambda}_j - 1)/\delta$ as the weighted growth rate of species j,

$$\tilde{\lambda}'_j = \frac{Y_j(1 - d)(1 - \alpha_j)}{C_j} + d\left(\frac{N_j Y_j(1 - \alpha_j)}{C_j} + \sum_{k \neq j} \frac{N_k Y_j}{C_k}\right) - 1.$$

(A.4)

We can thus calculate stabilizing mechanism and mean fitness-differences using $\tilde{\lambda}'_j$.

Approximating the probability of recruitment
Next, we simplify the terms $Y_j(1 - \alpha_j)/C_j$ and Y_j/C_k, which represent recruitment probabilities in conspecific and heterospecific sites. By eqn (1), C_j is essentially an N_j-weighted mean of the Y_j terms, reduced slightly by CNDD. Because the Y_j terms are similar, and the α_j terms are small, $Y_j(1 - \alpha_j)/C_j$ and Y_j/C_k will be close to 1. Thus, we can use the approximation $X/Y \approx 1 + \ln X - \ln Y$, and find that

$$\frac{Y_j(1 - \alpha_j)}{C_j} \approx 1 + \ln Y_j + \ln\{1 - \alpha_j\} - \ln C_j,$$

$$\frac{Y_j}{C_k} \approx 1 + \ln Y_j - \ln C_k,$$

(A.5)

(Stump & Chesson 2015). Because α_j is small,

$$\ln\{1 - \alpha_j\} \approx -\alpha_j.$$

(A.6)

Next we approximate $\ln C_j$. Defining $\bar{Y}$ as the mean yield across species, and $Y_j' = Y_j/\bar{Y}$ as the amount that Y_j differs from the mean,

$$\frac{C_j}{\bar{Y}} = Y_j'(1 - d + dN_j)(1 - \alpha_j) + \sum_{k \neq j} Y_k' dN_k.$$

(A.7)

We will next approximate $C_j/\bar{Y}$ using a first-order Taylor series approximation around $\alpha_j = 0$ and $Y_j' = Y_k' = 1$, and get that

$$\frac{C_j}{\overline{Y}} \approx 1 + (Y_j' - 1)(1 - d + dN_j) + \sum_{k \neq j}(Y_k' - 1)dN_k - (\alpha_j - 0)(1 - d + dN_j).$$

$$= 1 + (Y_j' - 1)(1 - d) + \sum_{\text{all } k}(Y_k' - 1)dN_k - \alpha_j(1 - d + dN_j),$$

(A.8)

where the latter summation is over all S species (including j). Since Y_j does not differ from the average by much, we can substitute in $Y_j' \approx 1 + \ln\{Y_j\} - \ln\{\overline{Y}\}$, and our equation simplifies to

$$\frac{C_j}{\overline{Y}} \approx 1 + \ln\{Y_j\}(1 - d) + \sum_{\text{all } k}\ln\{Y_k\}dN_k - \ln\{\overline{Y}\} - \alpha_j(1 - d + dN_j).$$

(A.9)

We then simplify the left hand side with the approximation X/Y ≈ 1+ ln X − ln Y, and find that

$$1 + \ln\{C_j\} - \ln\{\overline{Y}\} \approx 1 + \ln\{Y_j\}(1 - d) + \sum_{\text{all } k}\ln\{Y_k\}dN_k - \ln\{\overline{Y}\} - \alpha_j(1 - d + dN_j).$$

(A.10)

Thus,

$$\ln C_j \approx \ln\{Y_j\}(1 - d) + \sum_{\text{all } k}\ln\{Y_k\}dN_k - \alpha_j(1 - d + dN_j).$$

(A.11)

For simplicity, we will define $\overline{\ln Y_k}^N$ as the abundance-weighted mean of $\ln\{Y_k\}$; thus

$$\ln C_j \approx \ln\{Y_j\}(1 - d) + d\,\overline{\ln Y_k}^N - \alpha_j(1 - d + dN_j).$$

(A.12)

Simplifying the finite rate of increase

Next, we use our approximations to rewrite $\tilde{\lambda}_j'$ as the sum of several additive components. Plugging approximations (A.5) and (A.6) into our equation for $\tilde{\lambda}_j'$, eqn (A.4), we find that

$$\tilde{\lambda}_j' \approx (1 - d + N_j d)(1 + \ln Y_j - \alpha_j - \ln C_j) + \sum_{k \neq j} N_k d(1 + \ln Y_j - \ln C_k) - 1.$$

(A.13)

Noting that the N_j terms must sum to 1 (since they are frequencies), and defining $\overline{\ln C}^N$ as the abundance-weighted mean of the $\ln C_j$ terms, this simplifies to

$$\tilde{\lambda}_j' \approx \ln Y_j - \alpha_j(1 - d + dN_j) - (1 - d)\ln C_j - d\,\overline{\ln C}^N.$$

(A.14)

Finally, substituting in our approximation for $\ln C_j$, eqn (A.12), this becomes

$$\tilde{\lambda}_j' \approx \ln Y_j - \alpha_j(1 - d + dN_j) - (1 - d)\left[\ln\{Y_j\}(1 - d) + d\,\overline{\ln Y_k}^N - \alpha_j(1 - d + dN_j)\right]$$
$$- d\,\overline{\ln C}^N.$$
$$= d(2 - d)\ln Y_j - \alpha_j d(1 - d + dN_j) - d\,\overline{\ln C}^N - d(1 - d)\overline{\ln Y_k}^N.$$

(A.15)

Partitioning invader growth rates

The stabilizing mechanism will be the mean of invader growth rates, $\tilde{\lambda}_i'$, across species. This could be calculated using eqn (A.15), except we cannot calculate $\overline{\ln C}^N$ or $\overline{\ln Y_k}^N$ without knowing the densities of each species. However, Chesson (1994) noted a useful property: all

species other than the invader (called the "residents") are at equilibrium, and thus $\tilde{\lambda}'_r = 0$ for all species other than the invader. Therefore, we can write the invader's growth rate as

$$\tilde{\lambda}'_i = \tilde{\lambda}'_i - \frac{1}{S-1}\sum_{r \neq i} \tilde{\lambda}'_r$$

(A.16)

(Chesson 2000). Plugging in approximation (A.15),

$$\tilde{\lambda}'_i \approx d(2-d)\ln Y_i - \alpha_i d(1-d+dN_i) - d\,\overline{\ln C}^N - d(1-d)\,\overline{\ln Y_k}^N$$
$$- \frac{1}{S-1}\sum_{r \neq i}\left(d(2-d)\ln Y_r - \alpha_r d(1-d+dN_r) - d\,\overline{\ln C}^N - d(1-d)\,\overline{\ln Y_k}^N\right).$$

(A.17)

The $\overline{\ln C}^N$ and $\overline{\ln Y_k}^N$ will cancel, since they are the same for all species. We can then partition $\tilde{\lambda}'_i$ into terms caused by yield, ΔY_i, and terms caused by CNDD, ΔP_i,

$$\tilde{\lambda}'_i \approx \Delta P_i + \Delta Y_i,$$

(A.18)

where

$$\Delta Y_i = d(2-d)\left(\ln Y_i - \frac{1}{S-1}\sum_{r \neq i}\ln Y_r\right),$$

(A.19)

and

$$\Delta P_i = -\alpha_i d(1-d) + \frac{1}{S-1}\sum_{r \neq i}\alpha_r d(1-d+dN_r).$$

(A.20)

Note that the N_i term was removed because $N_i = 0$. The term ΔP_i rearranges to

$$\Delta P_i = -d(1-d)\left(\alpha_i - \frac{1}{S-1}\sum_{r \neq i}\alpha_r\right) + \frac{d^2}{S-1}\sum_{r \neq i}\alpha_r N_r.$$

(A.21)

The term $\frac{1}{S-1}\sum_{r \neq i}\alpha_r N_r$ can be seen as the mean of $\alpha_r N_r$ across species. Thus, it can be rewritten as

$$\frac{1}{S-1}\sum_{r \neq i}\alpha_r N_r = \left(\frac{1}{S-1}\sum_{r \neq i}\alpha_r\right)\left(\frac{1}{S-1}\sum_{r \neq i}N_r\right) + \mathrm{cov}(\alpha_r, N_r)^{-i}$$

(A.22)

where $\mathrm{cov}(\alpha_r, N_r)^{-i}$ is the covariance of α_r and N_r across all residents when species i is the invader. Note that in a community with just two species (and therefore one resident), the covariance term will be 0 (i.e., the mean of $\alpha_r N_r$ will simply be α_r). The N_r terms must sum to 1 (since they are proportions), thus,

$$\Delta P_i = -d(1-d)\left(\alpha_i - \frac{1}{S-1}\sum_{r \neq i}\alpha_r\right) + \frac{d^2}{S-1}\left(\frac{1}{S-1}\sum_{r \neq i}\alpha_r\right) + d^2\mathrm{cov}(\alpha_r, N_r)^{-i}.$$

(A.23)

Additionally, we can simplify ΔY_j by expressing it in terms of a community average:

$$\Delta Y_i \approx d(2-d)\left(\ln Y_i - \frac{1}{S-1}\sum_{r \neq i}\ln Y_r\right)$$

$$= d(2-d)\left(\ln Y_i + \frac{\ln Y_i}{S-1} - \frac{\ln Y_i}{S-1} - \frac{1}{S-1}\sum_{r \neq i}\ln Y_r\right)$$

$$= d(2-d)\left(\frac{S}{S-1}\ln Y_i - \frac{1}{S-1}\sum_{\text{all }k}\ln Y_k\right)$$

$$= d(2-d)\left(\frac{S}{S-1}\ln Y_i - \frac{S}{S-1}\frac{1}{S}\sum_{\text{all }k}\ln Y_k\right).$$

(A.24)

Thus,

$$\Delta Y_i \approx \frac{Sd(2-d)}{S-1}\left(\ln Y_i - \overline{\ln Y}\right).$$

(A.25)

Calculating stabilizing and fitness effects of CNDD and yield

Finally, we calculate the stabilizing mechanisms and mean-fitness differences, starting with the effects of yield. The stabilizing effect of yield is

$$\overline{\Delta Y} = \frac{1}{S}\sum_{\text{all }k}\Delta Y_k.$$

(A.26)

This will some to 0, since the mean of $\left(\ln Y_i - \overline{\ln Y}\right)$ is $\left(\overline{\ln Y} - \overline{\ln Y}\right)$, which is 0. The mean fitness difference between species j and its competitors (i.e., $\Delta Y_j - \overline{\Delta Y}$, eqn (6)) is therefore just ΔY_j (i.e., eqn (A.25))

Next, we calculate the stabilizing effect of CNDD,

$$\overline{\Delta P} = \frac{1}{S}\sum_{\text{all }k}\Delta P_k.$$

(A.27)

The term $\left(\alpha_i - \frac{1}{S-1}\sum_{r \neq i}\alpha_r\right)$ in eqn (A.23) will sum to 0 across species (as with $\overline{\Delta Y}$, see eqn (A.24)). Similarly, the mean of $\left(\frac{1}{S-1}\sum_{r \neq i}\alpha_r\right)$ is $\overline{\alpha}$. Finally, our computer simulations suggest that the mean of $\text{cov}(\alpha_r, N_r)^{-i}$ across invaders is well approximated by $\text{cov}(\alpha_j, N_j)$ (calculated when all species are at equilibrium), Fig. S4a; the exception is in two-species communities, since $\text{cov}(\alpha_r, N_r)^{-i}=0$ when there is 1 resident. Thus, in a community with two species,

$$\overline{\Delta P} = d^2\overline{\alpha},$$

(A.28)

and in a community with $S \geq 3$ species,

$$\overline{\Delta P} = \frac{d^2\overline{\alpha}}{S-1} + d^2\text{cov}(\alpha_j, N_j).$$

(A.29)

This is eqn (4). To derive eqn (3) (the stabilizing effect when α_j does not vary between species), note that if α_j is constant across all species, then $\text{cov}(\alpha_j, N_j) = 0$.

Finally, the mean fitness-difference effect of CNDD on species j is

$$\Delta P_i - \overline{\Delta P} = \left(-d(1-d)\left(\alpha_i - \frac{1}{S-1}\sum_{r \neq i}\alpha_r\right) + \frac{d^2}{S-1}\left(\frac{1}{S-1}\sum_{r \neq i}\alpha_r\right) + d^2\text{cov}(\alpha_r, N_r)^{-i}\right)$$
$$-\left(\frac{d^2\bar{\alpha}}{S-1} + d^2\text{cov}(\alpha_r, N_r)\right).$$

(A.30)

Simulations suggest that the difference in the covariance terms will be small enough to ignore. To simplify the equation further, we will rewrite the $\frac{1}{S-1}\sum_{r \neq i}\alpha_r$ term in terms of $\bar{\alpha}$:

$$\frac{1}{S-1}\sum_{r \neq i}\alpha_r = \frac{\alpha_i}{S-1} - \frac{\alpha_i}{S-1} + \frac{1}{S-1}\sum_{r \neq i}\alpha_r$$
$$= -\frac{\alpha_i}{S-1} + \frac{1}{S-1}\sum_{\text{all } k}\alpha_k$$
$$= -\frac{\alpha_i}{S-1} + \frac{S}{S-1}\frac{1}{S}\sum_{\text{all } k}\alpha_k$$
$$= -\frac{\alpha_i}{S-1} + \frac{S}{S-1}\bar{\alpha}$$

(A.31)

Thus,

$$\Delta P_i - \overline{\Delta P} \approx -d(1-d)\left(\alpha_i - \left[-\frac{\alpha_i}{S-1} + \frac{S}{S-1}\bar{\alpha}\right]\right) + \frac{d^2}{S-1}\left(-\frac{\alpha_i}{S-1} + \frac{S}{S-1}\bar{\alpha}\right) - \frac{d^2\bar{\alpha}}{S-1}.$$

(A.32)

Many terms will cancel, and leaving

$$\Delta P_j - \overline{\Delta P} \approx \left(\bar{\alpha} - \alpha_j\right)\left(\frac{d(1-d)S}{S-1} + \frac{d^2}{(S-1)^2}\right).$$

(A.33)

This is eqn (5).

In the main text, we argue that if there are no yield differences, and if $d=1$, then species are guaranteed to coexist. To see this, note that when yield differences are absent, then an invader's growth rate is simply ΔP_i; and, when $d=1$, then by eqn (A.20),

$$\tilde{\lambda}_i' \approx \frac{1}{S-1}\sum_{r \neq i}\alpha_r N_r.$$
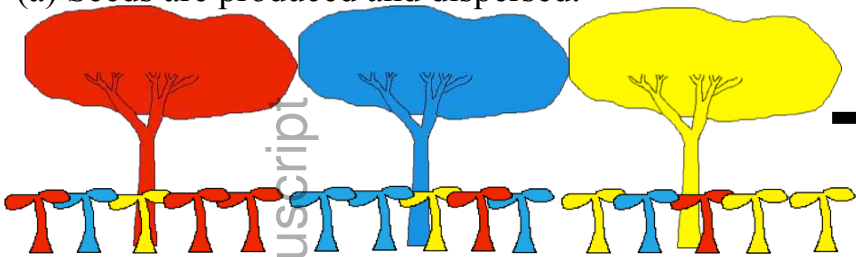
(A.34)

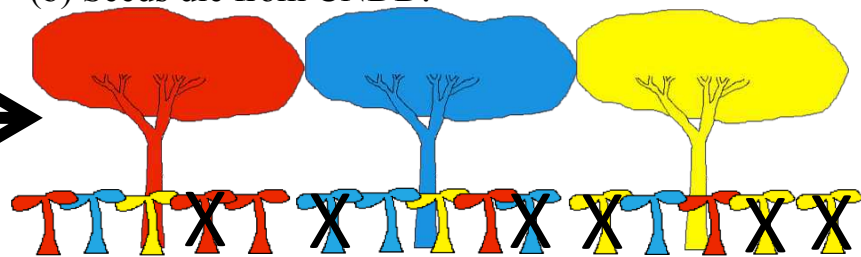This will always be positive whenever $\alpha_j > 0$ for all j.

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(a) Seeds are produced and dispersed.

(b) Seeds die from CNDD.

(c) Adults die.

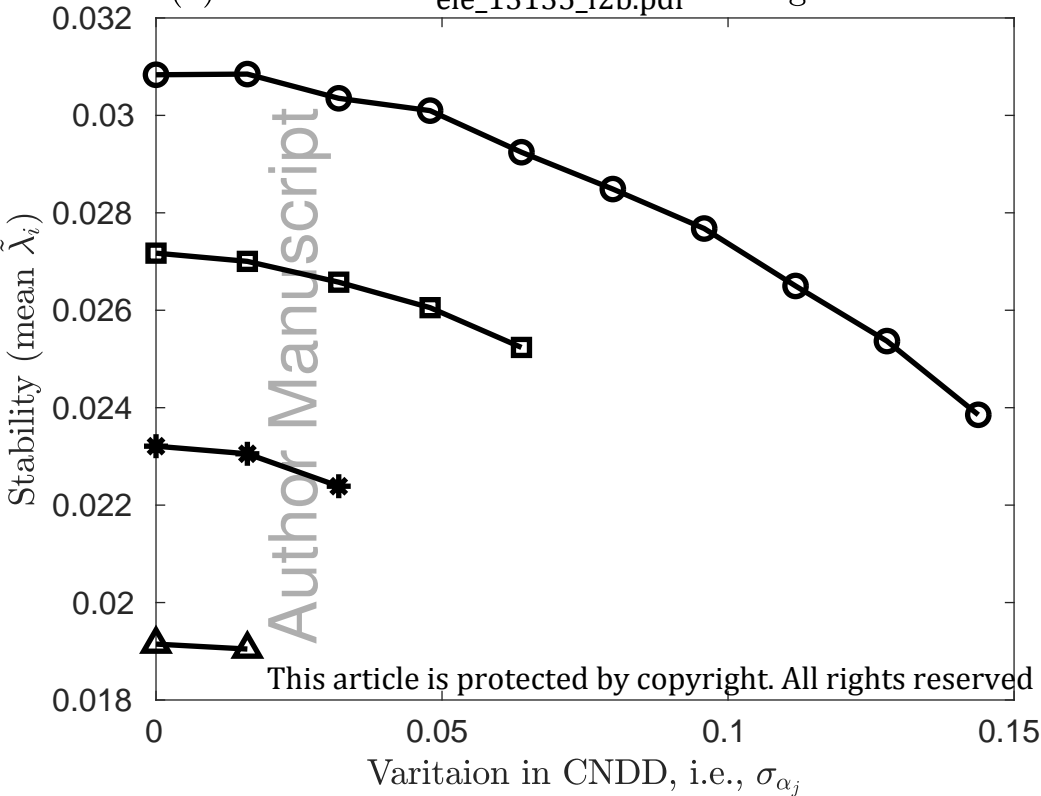(d) Lottery competition to capture gaps.

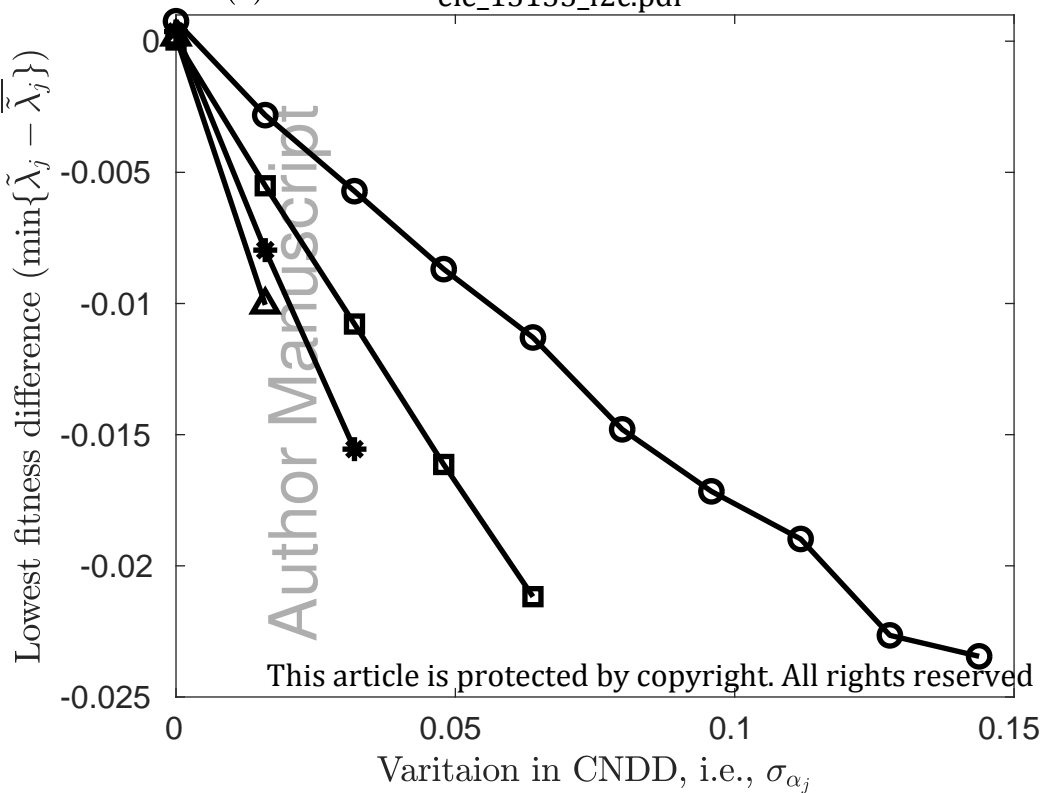(a) Variation in CNDD affects species richness
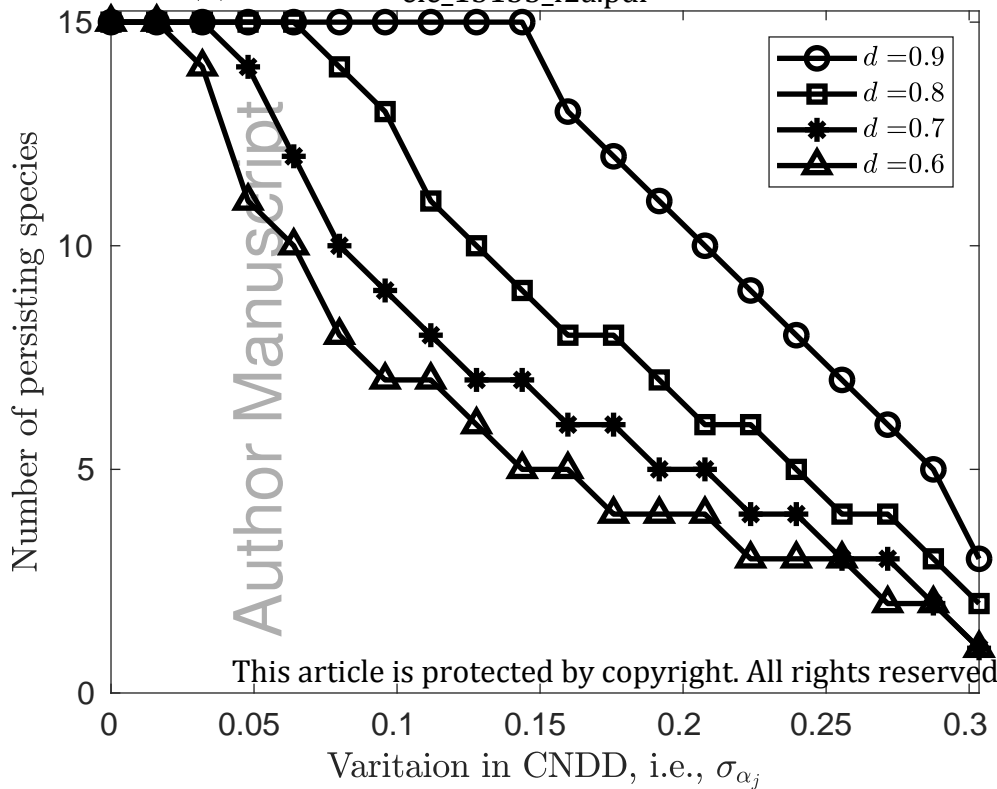
ele_13135_f2a.pdf

Legend:
- $d = 0.9$ (○)
- $d = 0.8$ (□)
- $d = 0.7$ (*)
- $d = 0.6$ (△)

X-axis: Varitaion in CNDD, i.e., σ_{α_j}

Y-axis: Number of persisting species

(b) Variation in CNDD affects stabilizing mechanisms

ele_13135_f2b.pdf

Stability (mean $\tilde{\lambda}_i$)

Varitaion in CNDD, i.e., σ_{α_j}

(c) Variation in CNDD affects fitness-differences
ele_13133_f2c.pdf

y-axis: Lowest fitness difference $(\min\{\tilde{\lambda}_j - \overline{\tilde{\lambda}_j}\})$

x-axis: Varitaion in CNDD, i.e., σ_{α_j}

(a) How fast species are lost in each community

Legend:
- different CNDD, α_j (magenta triangles)
- different yield, Y_j (green circles)

X-axis: Variation in CNDD (or yield equivalent)

Y-axis: mean(ln(time to 1st species lost))

(b) Number of species maintained in each community

ele_13135_f3b.pdf

(c) Community evenness

(a) Abundance vs. growth, α_j varies

Growth rate, $\tilde{\lambda}_j$

Abundance, N_j

(b) Abundance vs. growth, Y_j varies

ele_13135_f48.pdf
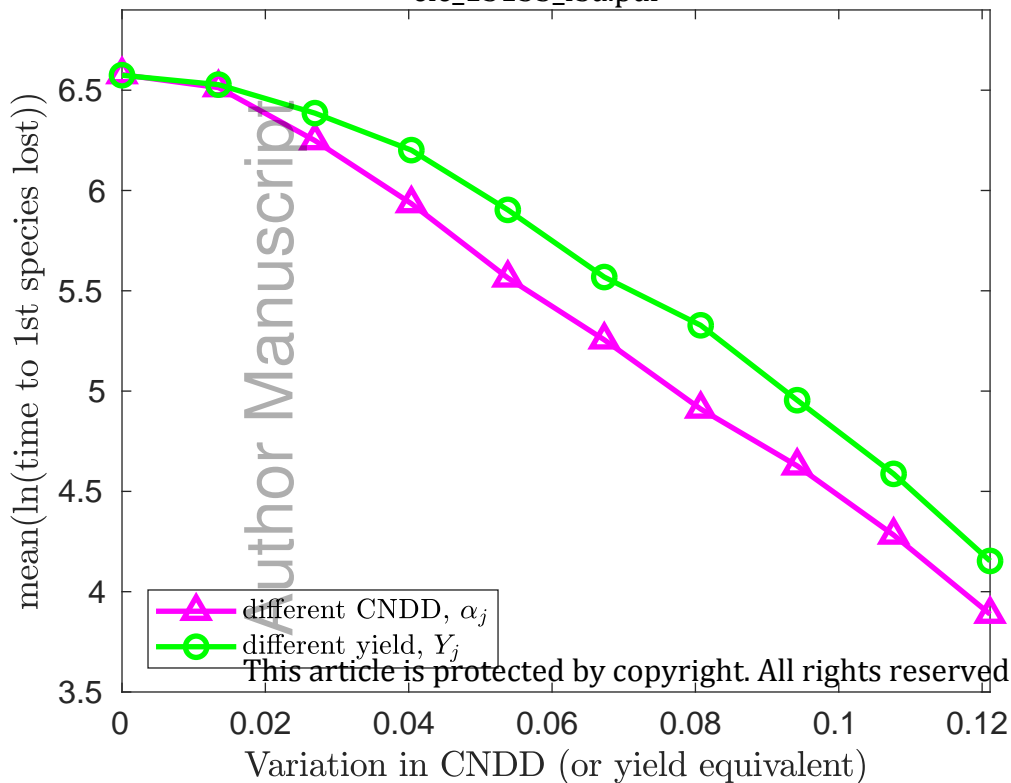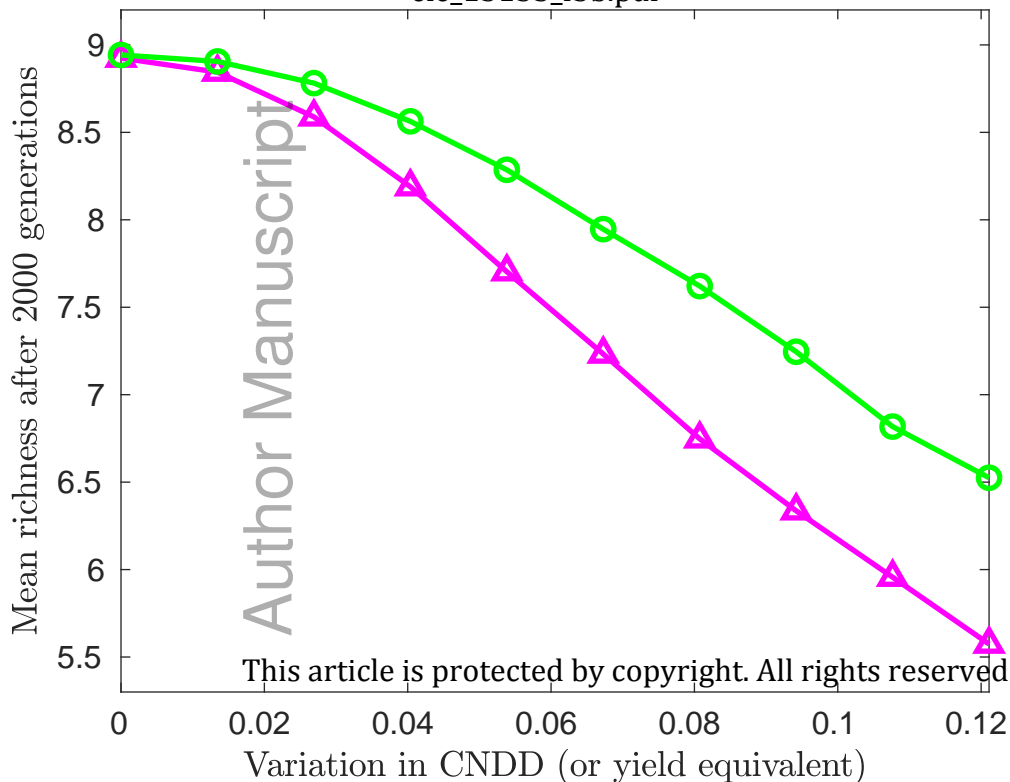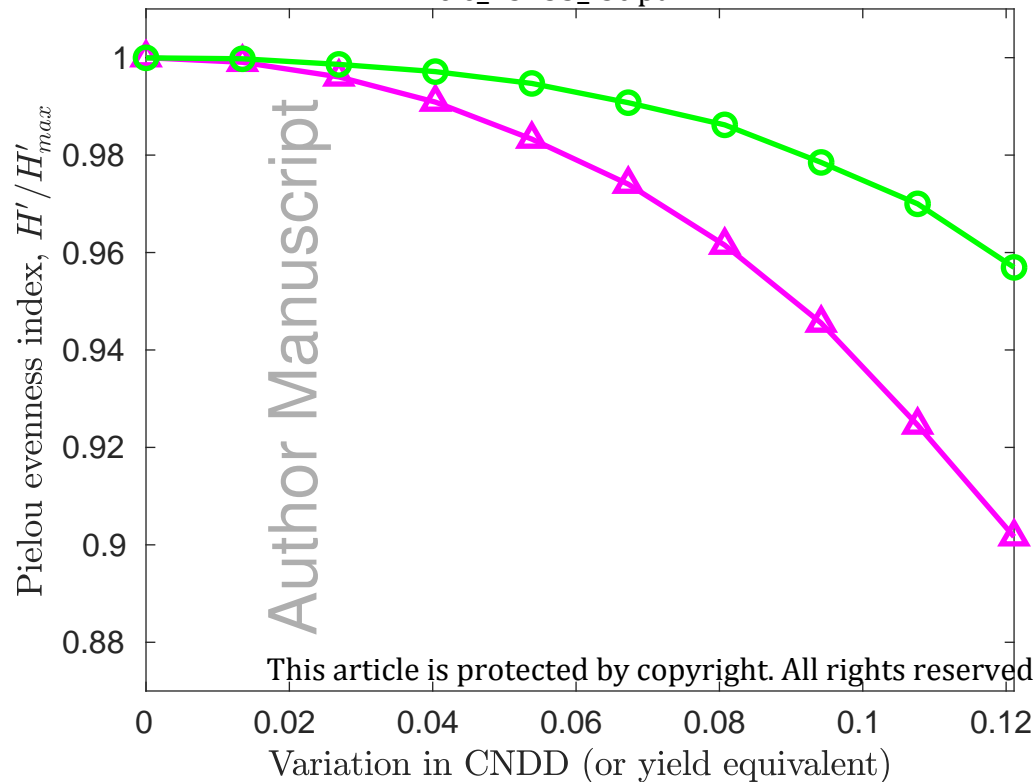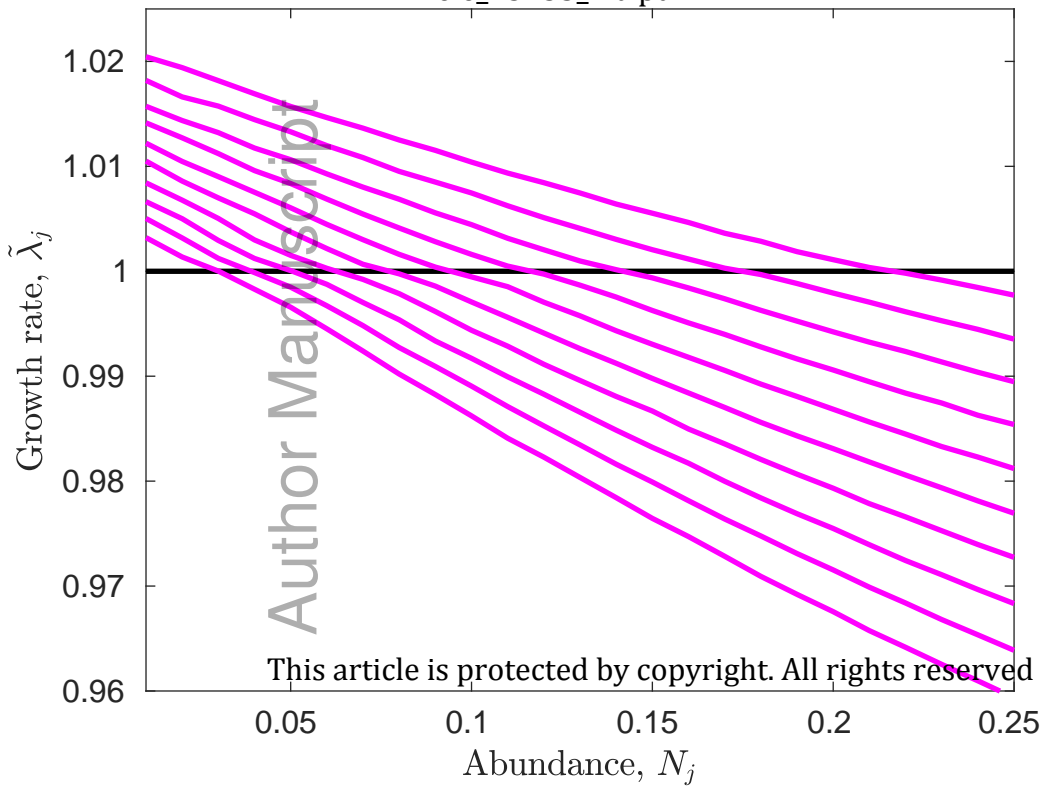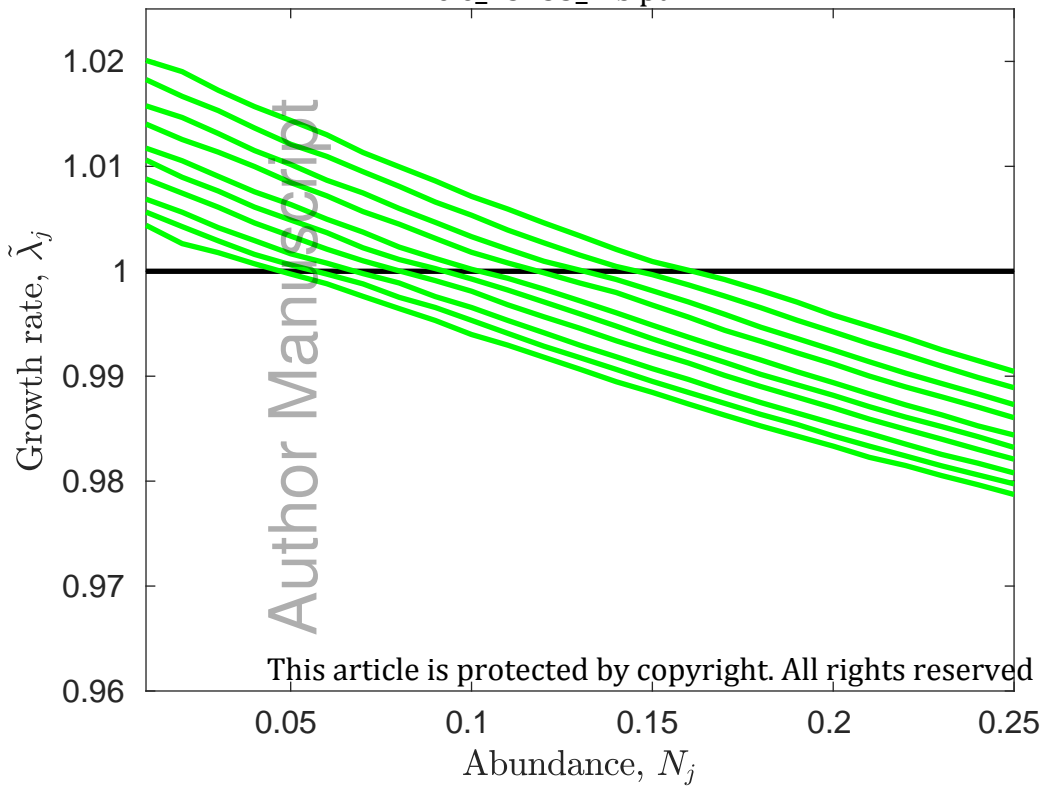
(a) Data from Comita et al. (2010)
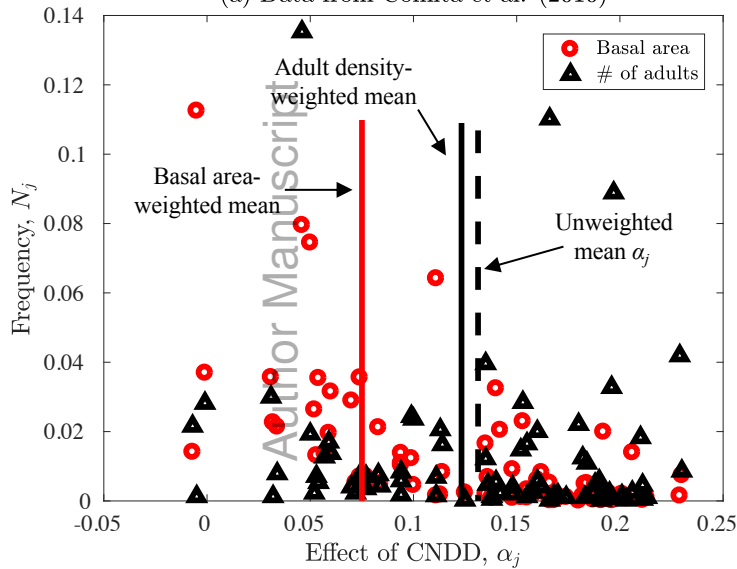
(b) Number of spp. maintained by CNDD

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Legend:
- Basal area (red)
- # of adults (black)

Y-axis: Number of species with $\Delta P_j > 0$

X-axis: Dispersal fraction, d

(c) Histogram of ΔP_j

ele_13135_f5c.pdf

- decreased growth rate
- increased growth rate

Legend:
- $d = 0.95$
- $d = 0.8$

Y-axis: Fraction of species

X-axis: Effect of CNDD on invader growth, ΔP_j