Trophic downgrading decreases species asynchrony and community stability regardless of climate warming

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ABSTRACT

Theory and some evidence suggest that biodiversity promotes stability. However, evidence of how trophic interactions and environmental changes modulate this relationship in multitrophic communities is lacking. Given the current scenario of biodiversity loss and climate changes, where top predators are disproportionately more affected, filling these knowledge gaps is crucial. We simulated climate warming and top predator loss in natural microcosms to investigate their direct and indirect effects on temporal stability of microbial communites. We also investigated the role of underlying stabilizing mechanisms on community stability. Community stability was insensitive to warming, but indirectly decreased due to top predator loss via increased mesopredator abundance and consequent reduction of species asynchrony and stability. The magnitude of destabilizing effects differed among trophic levels, being disproportionally higher at lower trophic levels (e.g. producers). Our study unravels major patterns and causal mechanisms by which trophic downgrading destabilizes large food webs, regardless of climate warming scenarios.

INTRODUCTION

Anthopogenic impacts on ecosystems have culminated in biodiversity loss worldwide, potentially compromising ecosystem functioning and stability (Hooper *et al.* 2012, Hautier *et al.* 2015). Unraveling major drivers of diversity-stability relationships (hereafter as DSRs) has been an urgent issue for ecologists (McCann 2000; Ives & Carpenter 2007; Donohue *et al.* 2013), since stable communities are less prone to extinctions and subsequent species invasions, providing more reliable ecosystem services (Pimm 1984; Hooper *et al.* 2005). It is known that temporal stability of community-level properties (hereafter as community stability) and DSRs are driven by different ecological processes that can be influenced by increasing species diversity. First, community stability is positively influenced by overyielding effects, i.e., the increase on mean productivity (abundance or biomass) of community, which are commonly present in more diverse communities due to niche complementarity effects (Valone & Hoffman 2003; Isbell *et al.* 2009; Hector *et al.* 2010). Second, community stability is responsive to portfolio effects, when the variability of an attribute is lesser on an aggregated component than on their components individually (Tilman 1999). Sometimes, this phenomenon is caused by statistical averaging, i.e., the sum of a set of a random and independent fluctuations is more stable when there are more variables summed (Doak *et al.* 1998). However, portfolio effects also can be driven by greater population stability of the constituent species *per se* (hereafter as species stability), which directly contributes to aggregate community-level, as well as the presence of asynchronous patterns in the population dynamics (Thibaut & Connolly 2013, Loreau & de Mazancourt 2013). Asynchrony involves compensatory dynamics and insurance effects facing disturbances when some species respond positive to an environmental change and others respond negatively (Yachi & Loreau 1999; Gonzalez & Loreau 2009). Species asynchrony can be enhanced with greater species richness by increasing the diversity of species' responses to

69   disturbances and environmental variability (Loreau & de Mazancourt 2013). A growing body of

70   evidence has reported positive DSRs on natural communites (Ives & Carpenter 2007; Tilman *et*

71   *al.* 2014). Nevertheless, current reviews revealed that, despite being present, DSRs also can be

72   relatively weak in many ecosystems (Campbell *et al.* 2011; Houlahan *et al.* 2018). Moreover,

73   DSR research is considerably skewed by approaches focused only on species richness

74   manipulation in single trophic levels, usually plant communities (Tilman *et al.* 2014; Pires *et al.*

75   2018). However, DSRs differs in multitrophic systems (Jiang & Pu 2009), such that strength and

76   direction of diversity-related effects can be strongly modulated by trophic interactions (Thébault

77   & Loreau 2005; Jiang *et al.* 2009).

78   Climate warming is among the most pervasive factors of biodiversity loss (Sala *et al.*

79   2000), with forecasts of more pronounced changes for the next decades (MEA 2005; IPCC 2014).

80   Climate warming influences biodiversity by modifying species physiology, phenology and

81   distribution, besides decoupling species interactions and shifting community species composition

82   (Parmesan 2006; Walther *et al.* 2010). Consequently, warming is able to modulate stabilizing

83   mechanisms. It can increase or decrease the community productivity (Yvon-Durocher *et al.* 2011,

84   2015) or even modify species dynamics, decreasing both species stability and species asynchrony

85   (Yang *et al.* 2016; Ma *et al.* 2017). Furthermore, reviews report that positive DSRs are weaker in

86   response to climatic stressors such as climate warming (De Boeck *et al.* 2018; Pires *et al.* 2018).

87   However, research manipulating experimentally future climate warming scenarios are relatively

88   recent (e.g. Kratina *et al.* 2012; Ma *et al.* 2017, Antiqueira *et al.* 2018a,b) and, consequently,

89   overall effects of climate warming on temporal stability remains unclear.

90   Trophic downgrading, i.e., the disproportionate extinction of higher trophic level

91   species (e.g. top predators), represents another critical threat to ecosystems worldwide (Estes *et*

92   *al.* 2011). Top predators are important modulators of trophic cascades and can determine

93   productivity, structure, diversity and dynamics of food webs (Finke & Denno 2004; Estes *et al.*

94   2011; Cardinale *et al.* 2012). Vertical diversity (i.e. number of trophic levels on a food web, see

95   Duffy *et al.* 2007) is also crucial for ecosystem functioning and stability because several

96   ecosystem functions respond at different trophic levels, which are mutually modulated by

97   cascading effects through their trophic interactions (Soliveres *et al.* 2016). DSR research

98   manipulating predator-prey interactions reported that stability of prey populations is highly

99   sensitive to predator loss (Halpern *et al.* 2005; Jiang *et al.* 2009) and variability of predator

100 dynamics (Mrowicki *et al.* 2016), both for small trophic modules (Jiang *et al.* 2009) and for

101 larger food webs (O'Gorman & Emmerson 2009; Donohue *et al.* 2013). Although higher trophic

102 levels are more vulnerable to environmental changes (Petchey *et al.* 1999; Voigt *et al.* 2003;

103 Daufresne *et al.* 2009), their predation pressure can be enhanced with warming to compensate

104 higher metabolic demands (Rosemblatt & Schmitz 2016, Romero *et al.* 2018). Thus, their net

105 effects on trophic dynamics can vary from weak (Fussmann *et al.* 2014) to strong with warming

106 (Rosemblatt & Schmitz 2016), leading to concerns about how overall climate warming affects

107 trophic cascades in multitrophic systems. Despite the advances in biodiversity research in

108 integrating climate and multitrophic approaches, there is still a lack of evidence on how these

109 factors interact, especially for tropical ecosystems (Marino *et al.* 2018).

110   We conducted a manipulative field experiment to investigate how climate warming

111 and top predator loss influence stability of total community abundance and of total abundance of

112 organisms in different trophic levels. We used tank-bromeliad as freshwater model systems,

113 focusing on responses of bromeliad microbiota communities with a multitrophic framework in

114 simulated current and future climate warming scenarios (Fig. 1a). Tank bromeliad microcosms

115 are abundant ecosystems in Neotropical forests and of great relevance by providing a wide range

116 of ecosystem services (Ladino *et al.* 2019). Given their small size and wide multitrophic

117 diversity, these microcosms allow high replicability in the field and easy manipulation of climatic

118 and biotic factors, with realistic responses to different scenarios of manipulation of these factors

119 (Antiqueira *et al.* 2018a,b; Bernabé *et al.* 2018). In addition, such systems allow short-term

120 experiments that include large numbers of generations, providing more reliable long-term

121 responses from community dynamics to different experimental stressors (Altermatt *et al.* 2015).

122   We predicted that both top predator loss and warming can decrease community

123 stability through different pathways mediated by changes in microbiota diversity (i.e. average

124 richness) or on trophic cascades via mesopredator diversity and abundance (Fig. 1b). Each

125 pathway can influence differently stabilizing mechanisms such as overyielding and portfolio

126 effects (i.e. species stability and species asynchrony). We expected that warming generally

127 weakens DSRs by imposing an environmental filter that excludes non-adapted species (Kratina *et*

128 *al.* 2017). In contrast, warming can either directly influence community stability positively by

129 promoting overyielding and negatively by suppressing portfolio effects. Moreover, top predator

130 loss can decrease community stability and DSR by releasing mesopredators (e.g. filter-feeders)

131 from top-down control. A weaker top-down control on mesopredators can lead to higher

132 predation pressure on microbiota via complementarity (i.e., via greater mesopredator richness)

133 and density-dependent effects (i.e., via greater mesopredator abundance) (Duffy *et al.* 2007).

134 Consequently, the greater exposition of microbiota to predation can decrease community stability

135 to suppress overyielding (Finke & Denno 2004) and portfolio effects (Jiang *et al.* 2009). It is also

136 expected that top predator loss leads to secondary extinctions (Donohue *et al.* 2017) that decrease

137 DSRs on each trophic level. We also expected an interactive effect of warming and top predator

138 loss on community stability. Specifically, warming can influence trophic interaction effects on

139 community stability by increasing metabolic demand and feeding rates, which culminates on

140 higher predation pressure on warmer scenarios (Rosemblatt & Schmitz 2016). Thus, the expected

141 top-down control by top predators in warmer scenarios can decrease the mesopredator impact on

142 microbiota stability. Moreover, warming can also enhance consumption effects of mesopredators

143 on the microbiota and consequently amply destabilizing effects.

144   We found that top predator loss decreases stability at both community and trophic

145 group levels, while warming has no overall effect. Contrary to our predictions, microbial

146 community stability was more sensitive to mesopredator outbreak than changes on its species

147 richness. In general, our results showed top predator loss decreases indirectly community stability

148 by cascading effects on basal trophic groups, decreasing asynchrony on constituent species

149 dynamics due to increase of predation pressure by mesopredators.

150 **METHODS**

151 **Experimental Design**

152   Our study simulated different scenarios of global changes (global warming and

153 trophic downgrading) affecting the temporal stability of microorganism communities in

154 freshwater phytotelmata ecosystems. Details about our study area and system model are

155 presented in the Appendix S1. Prior to the experiment, we washed 30 *Neoregelia johanni*s

156 bromeliads and treated them with 5% sodium hypochlorite and antibiotics to exterminate all

157 macroinvertebrates and microbiota. Then, they were washed again using clean water, measured

158 and taken to the field for experimentation. The initial communities for each bromeliad were

159 established by collecting water and macrofaunal individuals of 15 wild *Neoregelia johannis*. We

160 planted and grouped the experimental plants in blocks according to plant volume, with six

161 bromeliads per block (Antiqueira *et al*. 2018a,b).

162   We randomly selected six bromeliads per block to receive the treatments distributed

163 in two main factors: warming and predator loss, and interaction between these factors, in a total

164   of five blocks. The top predator loss factor had two levels: (i) predator presence, composed for

165   three larvae of *Leptagrion andromache*, the most common top predator species in our system;

166   and (ii) predator absence. After 30 days of experiment, three new individuals were added in each

167   bromeliad to compensate for potential predator deaths.

168   The warming treatment was composed of three levels related to climate warming

169   prediction models (IPCC 2014; PBMC 2015): (1) ambient temperature (control); (2) 2ºC above

170   ambient temperature (expected for 2040); and (3) 4ºC above ambient temperature (expected for

171   2100). To simulate the warming scenarios we used a warming system and technology described

172   in Antiqueira *et al.* (2018a,b). See details in the Appendix S2.

173   **Community Sampling**

174   To sample the microfauna, we collected 2mL of water samples per bromeliad at 0, 30,

175   50 and 75 days. These samples were fixed with acid 5%-iodine Lugol's solution and separated

176   into two subsamples: 1.5mL for phytoplankton analyses, and 0.5mL for zooplankton analyses.

177   Zooplankton samples were stained with Rose Bengal's aqueous solution to evidence complex cell

178   details like nucleus or cilia. We separated 100 μL of each sample and counted all organisms and

179   respective species under an optical microscope (Olympus BX51) with a camera attached for

180   greater visualization and photo storage. In order to obtain a more robust measure of species

181   richness, the remaining 400μL were diluted until 1mL distilled water and analyzed in a

182   Sedgewick-Rafter counting chamber to record rare morphospecies or that one which not appeared

183   in the first counting procedure. The total density of organisms per mL was estimated by

184   extrapolation. The phytoplankton subsamples were counted in an inverted microscope (Carl Zeiss

185   Axiovert 135) following estimate methods proposed by Utermöhl (1958) after sedimentation

186 method proposed by Lund *et al.* (1958). All sampled individuals were identified to the lowest

187 taxonomic level possible (species or morphospecies).

188 The bromeliads were also dissected at the end of the experiment (75 days) and each

189 leaf was washed to collect the whole content and to sample the macrofauna. We put the liquid

190 from the washing in white trays to facilitate the screening and so collected all macroinvertebrates.

191 We fixed them with 70% alcohol solution, identified at the lowest taxonomic level possible and

192 then counted and recorded the number of individuals and species (Antiqueira *et al.* 2018a,b).

193 **Trophic Groups and Food Web**

194 We separated the microbiota species in trophic categories according to their feeding

195 habits and trophic functional grouping (Appendix S3): (a) Producers: all autotrophic organisms,

196 such as flagellates, algae and cyanobacteria; (b) Primary Consumers: corresponds to

197 bacterivorous, algivorous or detritivorous species (composed mainly by heterotrophic flagellates

198 and some morphospecies of ciliates and testate amoebas); and (c) Secondary Consumers:

199 omnivorous or predator morphospecies (ciliates and testate amoebas, rotifers, copepods and

200 others). We determined Culicidae larvae (Appendix S4) as mesopredators, according to previous

201 studies using microfaunal communities (Brouard *et al.* 2011; Trzcinski *et al.* 2016)

202 **Diversity, temporal stability and stabilizing mechanisms**

203 We worked with ecological properties at two ecological organization levels: the

204 aggregate community and trophic levels. The aggregate community level was the set of all

205 morphospecies belonging to microbiota, while each trophic level was defined by grouping of

206 microbiota morphospecies belonging to their respective trophic level defined above. Microbiota

207 diversity was measured as average species richness over experimental time. Mesopredator

208   abundance and richness were recorded as total sampled values of Culicidae and detritivore

209   abundance and species richness recorded in the last experimental period.

210   The temporal stability (S) was estimated by the inverse of the coefficient of variation

211   (CV), where CV is the ratio between the standard deviation of density of all monthly samplings

212   (σ) and the mean of density of all monthly samplings (μ), multiplied by 100:

213
$$S = 100 \ \frac{1}{CV} = 100\left(\frac{\mu}{\sigma}\right)$$

214   We used average density over time as proxy for productivity (see Striebel *et al.* 2012) and

215   evaluated the presence of overyielding effects when increased diversity promoted indirectly

216   greater stability via increasing average density (Tilman 1999). Following an approach used by

217   Thibaut & Connolly (2013), we measure species stability (S_{sp}) as the weighted average

218   population stability: the inverse of mean CV of density of all constituent species within the

219   community, weighted by their relative densities, multiplied by 100, as:

220
$$S_{sp} = 100\left(\sum_i \frac{\mu_i}{\mu} \frac{\mu_i}{\sigma_i}\right)$$

221   With μ_i representing the mean of density of population of a species *i*, σ_i the standard deviation of

222   populational density of species *i* and μ the mean of density referring to aggregate community or

223   total population of a single trophic level. We measured species asynchrony adapting a measure of

224   synchrony developed by Loreau and de Mazancourt (2008), which compares the variance of

225   community level density with the summed variance of density of individual components. It is

226   calculated as:

227
$$\phi = \frac{\sigma^2}{\left(\sum_i \sigma_i\right)^2}$$

228 where ϕ represents the species synchrony, σ^2 is the variance of density of aggregate community

229 and σ_i is the standard deviation of density for a species i in this community. Our measure for

230 asynchrony $(1 - \phi)$ is standardized between 0 (perfect synchrony) and 1 (perfect asynchrony). We

231 calculated this metric using the "*synchrony*" function of "*codyn*" package in R (Hallett *et al.*

232 2016; R Core Team 2017).

Statistical Analyses

234   Linear mixed effect models (Pinheiro & Bates 2000) were used to evaluate main and

235 interactive effects of warming and top predator loss on mesopredator metrics (i.e. abundance and

236 richness of Culicidae), microbiota average species richness, proxies of stabilizing mechanisms

237 (i.e. average density, species stability, and asynchrony index) and temporal stability (S) for each

238 trophic level and at aggregate community level. For the different ecological variables used in this

239 study, we also tested the partial contribution of the values attributed to each trophic level to the

240 values measured at the community level. Warming was included as the temperature average of

241 each bromeliad (temperature recorded every hour over the experimental period) and was

242 considered as an independent continuous variable. Warming and predator presence/absence were

243 used as fixed effects and block was used as random effect. To meet homoscedasticity and

244 normality assumptions of LME models, we log10 transformed values for Culicidae abundance,

245 average density, species stability and stability to the aggregate community level and for each

246 trophic level.

247   We conducted piecewise structural equation models (SEMs) to investigate the direct and

248 indirect effects of warming and top predator loss on temporal stability of community and

249 different trophic levels via changes on mesopredator metrics, microbiota diversity and stabilizing

250 mechanisms. We also evaluated how stability of higher trophic levels influenced stability of

251 lower ones on microbial food web, as well as the food web stability responded to the

252 experimental drivers. We fitted the SEMs using the *piecewiseSEM* package in R (Lefcheck 2016;

253 R Core Team 2017). Warming and top predator loss were included as exogenous variables.

254 Mesopredator metrics, microbiota diversity, stabilizing mechanisms and temporal stability (S)

255 were included as endogenous continuous variables. We built all models using LMEs, considering

256 block as a random effect. To measure the differential contribution of complementarity or density-

257 dependent effects (associated with mesopredators) to community stability, we set up two different

258 pathing structures for each type of model (i.e. community or food web levels), so that each one

259 has only one mesopredator attribute (abundance or richness) as an intermediate endogenous

260 variable.

261   Given the absence of interactive effects of warming and top predator loss on any

262 endogenous variables (Table S1), we built the SEMs without interaction terms (Tables S2-S4). In

263 a similar way, we also built the SEMs without direct links of experimental drivers on stabilizing

264 mechanisms and temporal stability (S) at any ecological organization level (Tables S2-S4). We

265 reduced the number of non-significant paths and variables of SEMs via backward selection, using

266 Akaike Information Criteria corrected for small sample size (AICc).

267   We considered ΔAICc>2 units to distinguish models. To examine the presence of

268 multicollinearity in each model component, we calculated the variance inflation factor (VIF),

269 considering the presence of collinearity to VIF>3 (Zuur *et al*. 2010). SEM fit was tested through

270 of Shipley's test of d-separation using Fisher's C statistic, with adequate fits to p-values>0.05.

271 Squared and unsquared terms of community and producer asynchrony were added on SEMs to

272 control non-linear relationships and were mean centered to reduce collinearity (see Cardinale *et*

273 *al*. 2009). We also recorded values of AICc and the standardized coefficients (β) for each path of

274   each SEM. Indirect effects (β_{ind}) were estimated by the product of the significant β coefficients

275   along the paths.

276   **RESULTS**

277   Top predator loss was the strongest experimental driver of temporal stability of

278   bromeliad microbiota at community level, while warming did not show any direct or indirect

279   effect on community stability (Fig. 2, Fig. S1). Likewise, mesopredator abundance was the best

280   predictor for the community stability (Table S2). The SEM models did not detect direct effects of

281   microbiota community richness neither of any mesopredator metrics on community stability,

282   which were removed via AICc selection (Table S2). They also did not detect indirect effects of

283   community richness on community stability via any stabilizing mechanisms (Fig. 2, Fig. S1).

284   However, mesopredator abundance decreased indirectly community stability via decreasing

285   species asynchrony (Fig. 2a; β_{ind} = -0.410) and species stability (Fig. 2a; β_{ind} = -0.226).

286   Mesopredator abundance and richness increased with top predator loss, but did not respond to

287   warming (Fig. 2, Fig. S1). Thus, top predator loss decreased indirectly community stability via

288   increasing mesopredator abundance and consequent reduction of species asynchrony (Fig. 2a; β_{ind}

289   = -0.401) and species stability (Fig. 2a; β_{ind} = -0.221). Moreover, the response pattern of

290   community stability varied among stabilizing mechanisms. Community stability increased

291   exponentially and linearly with species asynchrony (Fig. 2b) and species stability (Fig. 2c),

292   respectively. However, it did not respond significantly to average community density (Fig. 2d).

293   In the case of stability of different trophic levels, we built SEM models that (i)

294   incorpored effects of multiple trophic levels simultaneously (Figs. 3a,b) or (ii) were related to

295   effects on each trophic level individually, focusing on the response of each level to the predictors

296   and underlying mechanisms (Figs. 3c,d). In all these models, we find a pattern similar to that seen

297 previously at the community level: top predator loss exerted strong indirect effects on stability, in

298 contrast to the absence of overall effects of warming (Fig. 3). Thus, we removed via AICc

299 selection the warming effect on multiple level SEM models (Table S3). We also did not find

300 significant direct effects of average richness or mesopredator metrics on stability of trophic

301 levels, which also were removed via AICc selection (Table S4).

302   There was no evidence of significant effects of stability of higher trophic levels on

303 the stability of lower levels (Fig. 3). However, each trophic level responded differently to top

304 predator loss, according to the predictor that most influenced each level. Producer stability

305 indirectly decreased with the top predator loss through an increase in mesopredator abundance

306 that directly decreased the producer stability (Fig.3a; β_{ind} = -0.552). In the SEM model for

307 producers, we detected indirect effects of mesopredator abundance on producer stability via

308 producer species stability (Fig. 3c; β_{ind} = -0.224) and producer species asynchrony (Fig. 3c; β_{ind} =

309 -0.408). Thus, similar to what was found at the community level, top predator loss decreased

310 producer stability indirectly by decreasing both species stability (Fig. 3c; β_{ind} = -0.219) and

311 asynchrony (Fig. 3c; β_{ind} = -0.398) at producer level, via increased mesopredator abundance. On

312 the other hand, primary consumer stability indirectly decreased with top predator loss via

313 increased mesopredator richness (Fig. 3b; β_{ind} = -0.612). Nevertheless, SEM model for primary

314 consumers showed no significant indirect effects of mesopredator richness on primary consumer

315 stability (Fig 3d), although all underlying mechanisms exerted strong positive direct effects on

316 stability in this trophic level (Fig 3d). Conversely, secondary consumer stability did not respond

317 directly or indirectly to mesopredator metrics neither indirectly to top predator loss (Figs 3a,b).

318   We found a disproportionate contribution from different trophic levels to the stability

319 of the microbiota community, so that producers strongly determined all ecological properties at

320 the community level. Producers explained (in terms of R^2) 98 to 99 percent of variation in

321 community-level properties as temporal stability (Fig. 4a) and the proxies for stabilizing

322 mechanisms (Fig. 4b-d), while primary consumers explained 34% of variation only for

323 community stability (Fig. 4a). In contrast, community average richness had a positive relationship

324 with average richness of all trophic levels of microbiota (Fig. 4e).

325 **DISCUSSION**

326 Our results bring new considerations about how predation influences stability in

327 speciose food webs. Community stability was more affected by density-dependent effects, i.e., it

328 was sensitive to higher predation pressure by mesopredators released via top predator loss.

329 Increase in mesopredator abundance induced stronger simultaneous declines on different prey

330 populations, leading to more unstable dynamics in the whole community. On other hand,

331 community stability also strongly responded to changes in very abundant trophic levels, such as

332 producers, which had a strong contribution on food web composition (74-99% of community

333 average density). Indeed, theory and empirical studies point that very abundant species can

334 provide stability in communities with high species dominance when such species present higher

335 resistance at disturbances and more stable dynamics (Hillebrand *et al.* 2008; Yang *et al.* 2016;

336 Ma *et al.* 2017). However, producers were the most vulnerable trophic level in our system,

337 responding strongly to predation by mesopredators. Despite being abundant, this higher

338 vulnerability of producers led to greater instability at the community level. These results

339 corroborate our predictions and previous evidence (O'Gorman & Emmerson 2009; Mrowicki *et*

340 *al.* 2016) that the loss of a single trophic level can trigger destabilizing effects over multiple

341 trophic groups on multitrophic communities. Depending on food web structure and which trophic

342 groups are affected, these indirect effects, which initially would destabilize only some trophic

343 groups, can in turn compromise the entire food web stability.

344   Our study reported similar patters of community stability response to predation found

345   in previous theoretical (Thébault & Loreau 2005) and empirical studies (Halpern *et al.* 2005;

346   Jiang *et al.* 2009), where predators can stabilize dynamics of basal trophic levels, such as

347   producers. However, while such studies were limited to effects of pairwise predator-prey

348   interactions or of trophic cascades in small food webs (i.e. with few trophic levels), we showed

349   how cascading effects of top predators, such as damselfly larvae, can trespass through various

350   intermediate trophic levels and influence basal trophic levels, such as the microbiota. That is,

351   predators seem to enhance stability in multiple trophic levels. Interestingly, these positive top-

352   down effects of top predators on community stability were also reported for other larger

353   freshwater ecosystems (Halpern *et al.* 2005) and even marine ecosystems (O'Gorman &

354   Emmerson 2009; Britten *et al.* 2014). Therefore, our findings highlight top predators as

355   consistent drivers of community stability in aquatic ecosystems, and also highlight the potential

356   risks of altering trophic cascades due to trophic downgrading for the stability of freshwater

357   ecosystems.

358   Among stabilizing mechanisms in our system, portfolio effects contributed

359   substantially more to enhance community stability, with emphasis on stronger and non-linear

360   effects of species asynchrony. Current theory (Loreau & de Mazancourt 2013) and empirical

361   evidence (Hector *et al.* 2010; Ma *et al.* 2017) show that asynchronous dynamics are commonly

362   driven by competitive interactions, diversity or environmental conditions. Conversely, our study

363   showed that species asynchrony can occur in response to changes in trophic interactions. Top

364   predator loss decreased indirectly, via mesopredator release, species asynchrony at both producer

365   and aggregate community levels, which were also intrinsically related to each other (Fig. 4b). It is

366   likely that increasing mesopredator abundance can intensify predation pressure on more

367   vulnerable species of producers and promote the selection of predation-resistant species, causing

368 greater synchrony. Moreover, top predator loss can also expand foraging areas to mesopredators

369 and consequently reduce potential spatial refuges for microbiota groups. These points could

370 explain how greater predation pressure by mesopredators influenced community stability

371 regardless of the absence of complementarity effects. Given the strong contribution of producers

372 to composition and dynamics at community level, our results suggest that the decrease in

373 community stability via top predator loss occurred mainly due to loss of compensatory dynamics

374 promoted by producer species asynchrony. In fact, we suggest that trophic cascades can act as

375 another major driver for species asynchrony in multitrophic communities.

376   Overyielding effects and productivity-stability relationships were negligible in our

377 study, thus contrasting with results found in other single and multitrophic systems (e.g. Jiang &

378 Pu 2009). Diversity-productivity relationships can be strongly altered by predators, with patterns

379 quite idiosyncratic varying among predation strategies and prey preferences (Duffy *et al.* 2007).

380 While more selective predators seem to promote overyielding effects and positive DSRs (Jiang *et*

381 *al.* 2009), our results suggest that non-selective filter-feeder mesopredators seem to exert

382 opposite effects, decreasing stability at different ecological organization levels but without

383 influencing their average densities. Even changes in species richness (promoted by warming and

384 top predator loss) did not exert significant effects on community average density in our system.

385 Indeed, our study emphatizes that sometimes overyielding can be an irrelevant mechanism for

386 community stability, depending on food web structure and composition. In contrast,

387 compensatory mechanisms (e.g. portfolio effects) seems to be more relevant, mitigating negative

388 effects of very productive species loss on the ecosystem productivity over time (e.g. via insurance

389 effects).

390   We did not observe overall effects of warming on community stability, which

391 contrast with earlier empirical evidences (Kratina *et al.* 2012; Yang *et al.* 2016, Ma *et al.* 2017).

392 Bromeliad communities suffer intense daily temperature variations (Antiqueira *et al.* 2018a),

393 leading to rapid adaptations in species with short generation time, such as microbiota (Geerts *et*

394 *al.* 2015). Moreover, recent meta-analysis suggested that top-down effects in ecosystems from

395 lower latitudes are less influenced by warming (Marino *et al.* 2018), a pattern found in our study.

396 Thus, these findings add new perspectives about the differential relevance between the effects of

397 trophic cascades against climate warming for the ecosystem functioning (Antiqueira *et al.* 2018b)

398 and stability on tropical freshwater ecosystems.

399   Our findings suggest that alterations on the vertical dimension of diversity can be a

400 stronger driver of DSRs than its horizontal component in complex and larger food webs. Previous

401 knowledge about the interactive effects of vertical and horizontal diversity in DSR research still

402 has many caveats to consider. For structural stability of food webs, vertical diversity does not

403 seem to operate as a stabilizing agent by itself, while diversity at multiple trophic levels plays as

404 a major driver for food web stability (Zhao *et al.* 2019). On the other hand, subtle changes in

405 vertical diversity seemed to directly influence the relationship between diversity and stability of

406 biomass of a single trophic group, changing the effect size and direction of species richness

407 (Jiang *et al.* 2009). In these cases, there was a direct impact of trophic interactions (either in their

408 strength or distribution) on the net effect of species richness on community stability, which could

409 be modified by adding or removing trophic levels. However, such previous studies that

410 manipulated species richness at multiple trophic levels restricted their approach to food webs

411 composed of a few (i.e., 2-3) trophic levels (e.g. Jiang *et al.* 2009; Zhao *et al.* 2019). Distinctly to

412 this evidence, we found in our system (composed by four to five trophic levels) that vertical

413 diversity loss was substantially more important for the community stability than the species

414 richness present in single or multiple trophic levels. In addition, the decrease of vertical diversity

415 resulted in trophic cascades that modified the effects of direct interactions between trophic groups

416 and influenced unevenly stability at multiple trophic levels. Moreover, we showed for the first

417 time that vertical diversity influenced stability by promoting compensatory mechanisms on

418 abundance dynamics. In agreement with previous evidence, this study reiterates the importance

419 of this vertical component in different measures of ecological stability.

420   Nevertheless, it remains difficult to make generalized predictions about the

421 importance of vertical diversity for stability on complex food webs. If a single dimension of

422 diversity (e.g. species richness) can influence multiple metrics of ecological stability in different

423 ways (Pennekamp *et al.* 2018), it is necessary that future research explores multifaceted

424 approaches to diversity and stability simultaneously, in order to understand how DSRs manifest

425 themselves in more complex and realistic food webs.

426   Our study identified consequences of altering climate patterns (via climate warming)

427 and trophic cascades (via top predator loss) for community stability in a tropical freshwater

428 ecosystem. While warming did not influence community stability, top predator loss triggered

429 several destabilizing cascade effects in properties of different trophic levels, which reverberated

430 throughout the whole food web. Stronger variations on the strength of trophic cascades can

431 modify profoundly several mechanisms of maintenance of stable conformations of food webs

432 (Piovia-Scott *et al.* 2017), which could compromise long-term fundamental relationships between

433 biodiversity and ecosystem functioning (Tilman *et al.* 2014; Soliveres *et al.* 2016). The decline of

434 a keystone predator species seems to provoke changes in several ecological properties at

435 community level in addition to stability, highlighting the recurrent threat of greater biodiversity

436 loss. Efforts to investigate causal mechanisms of how top predators determine stability in

437 different food webs must be increased in order to better predict how ecosystem processes and

438 services can be ensured under current biodiversity loss scenarios.

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644 **SUPPORTING INFORMATION**

645 Additional supporting information may be found online in the Supporting Information section at

646 the end of the article.

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659 **Figure captions**

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661 **Fig. 1: Experimental design and theoretical framework about influence of climate warming**

662 **and top predator loss on community stability. (a)** Illustration of main experimental

663 components on our bromeliad ecosystem, indicating the three warming scenarios used on the left

664 and the bromeliad food web composition below, distinguishing among the different trophic

665 groups. **(b)** Main predictions of direct and indirect effects of experimental warming and top

666 predator loss on different stabilizing ecological mechanisms (overyielding, species stability and

667 species asynchrony). The scheme represents how effects mediated by diversity (via species

668 richness) and trophic cascades (via mesopredator abundance and richness) determine community

669 stability by suppressing or enchancing stabilizing mechanisms. Blue, red and green arrows

670 indicate positive effects, negative effects and two possibilities, respectively.

671

672 **Fig. 2: Cascading effects of warming and top predator loss on diversity, stabilizing**

673 **mechanisms and community stability. (a)** Piecewise structural equation model (SEM) of direct

674 and indirect effects of experimental drivers on community stability, mediated by mesopredator

675 abundance. Solid black and red arrows represent significant ($p < 0.05$) positive and negative

676 paths, respectively. Light grey arrows represent non-significant paths ($p > 0.05$). The thickness of

677 the significant paths represents the magnitude of the standardized regression coefficient (β).

678 Marginal R^2s for component models are given on the boxes of endogenous variables.

679 Relationship between community stability and **(b)** community asynchrony (estimates: asynchrony

680 = - 0.69; asynchrony^2 = 1.33, p-value < 0.001, R^2 = 0.93), **(c)** species stability (estimate = 2.43, p-

681 value < 0.001, R^2 = 0.75) and **(d)** community average density (estimate = -0.2, p-value = 0.11)

682 are shown in the bottom panels. Significant regression lines are shown in red, with shaded area

683 representing 95% confidence interval. All Y axes are $\log_{10}$-scaled with untransformed values. X

684 axes of (c) and (d) are also $\log_{10}$-scaled.

685

686 **Fig. 3: Structural equation models of warming and top predator loss effects on**

687 **mesopredator attributes (abundance, richness) and temporal stability of trophic levels, and**

688 **underlying stabilizing mechanisms.** Paths constitute final models (after AICc model selection,

689 see Table SX) of direct effects of experimental drivers on each trophic level of the bromeliad

690 food web, with effects mediated by **(a)** mesopredator abundance and **(b)** mesopredator richness.

691   The subsequent SEMs (**c**, **d**) represent mechanistic pathways of influence of experimental drivers

692   on stability of **(c)** producers and **(d)** primary consumer. Solid black and red arrows represent

693   significant ($p < 0.05$) positive and negative paths, respectively. Light grey arrows represent non-

694   significant paths ($p > 0.05$). The thickness of the significant paths represents the magnitude of the

695   standardized regression coefficient (β). Marginal R^2s for component models are given on the

696   boxes of endogenous variables.

697   **Fig. 4: Contribution of each trophic level for different ecological properties and stability at**

698   **community level.** Panels show relationship between each trophic level and aggregate community

699   for **(a)** temporal stability (producer: estimate = 0.97, p-value < 0.001, R^2 = 0.99; primary

700   consumer: estimate = 0.71, p-value = 0.001, R^2 = 0.34; secondary consumer: estimate = 0.04, p-

701   value = 0.82), **(b)** species asynchrony: (producer: estimate = 0.96, p-value < 0.001, R^2 = 0.98;

702   primary consumer: estimate = 0.12, p-value = 0.465; secondary consumer: estimate = -0.24, p-

703   value = 0.376), **(c)** species stability (producer: estimate = 0.96, p-value < 0.001, R^2 = 0.98;

704   primary consumer: estimate = -0.002, p-value = 0.92; secondary consumer: estimate = -0.06, p-

705   value = 0.07), **(d)** average density (producer: estimate = 0.98, p-value < 0.001, R^2 = 0.998;

706   primary consumer: estimate = 0.14, p-value = 0.232; secondary consumer: estimate = 0.15, p-

707   value = 0.52) and **(e)** average richness (producer: estimate = 1.65, p-value < 0.001, R^2 = 0.75;

708   primary consumer: estimate = 2.28, p-value < 0.001, R^2 = 0.79; secondary consumer: estimate =

709   1.79, p-value < 0.001, R^2 = 0.33). Green, orange and purple elements represent producer, primary

710   consumer and secondary consumer, respectively. Solid lines indicate significant regression lines.

711   Shaded areas represent 95% confidence intervals. Y and X axes in (a), (c) and (d) are $\log_{10}$-scaled

712   with untransformed values.

713