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Predicting the impacts of co-extinctions on phylogenetic diversity in mutualistic networks

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Abstract

An important bias in the estimations of threatened evolutionary history is that extinctions are considered as independent events. However, the extinction of a given species may affect the vulnerability of its partners and cause extinction cascades. Co-extinctions are likely not random in the tree of life and may cause the loss of large amounts of unique evolutionary history. Here, we propose a method to assess the consequences of co-extinctions for the loss of evolutionary history and to identify conservation priorities. We advise considering both the complexity of the interaction networks and the phylogenetic complementarities of extinction risks among species. Using this approach, we demonstrated how co-extinction events can prune the tree of life using various species loss scenarios. As a case study, we identified pollinators for which extinctions would greatly impact plant phylogenetic diversity within local pollination networks from Europe. We also identified species features that may result in the highest losses of phylogenetic diversity. Our approach highlights the consequences of co-extinctions on the loss of evolutionary history and may help address various conservation issues related to co-extinctions and their impacts on biodiversity.

1. Introduction

Phylogenetic Diversity (PD) is now considered to be a key measure for conservation. In addition to representing the heritage of Earth, PD may also capture feature diversity and future benefits to society (i.e., option values) (Faith et al., 2010). The impact of the 6th extinction crisis on PD could be dramatic, especially when extinctions tend to be clustered in the tree of life (thus threatening not only terminal branches but also deep branches shared by the species at risk) or when species descending from long and isolated branches are threatened (Veron et al., 2016). However, previous assessments of at-risk PD considered extinctions as independent events (Faith, 2008; Jono and Pavoine, 2012) and did not account for possible co-extinctions (Dunn et al., 2009). A co-extinction is the extinction of a species as a consequence of its dependence on another that has gone extinct or declined below some threshold abundance (Colwell et al., 2012). In a recent study, Veron et al. (2016) reviewed the global loss of evolutionary history due to species extinctions in taxa such as mammals, birds, squamates, amphibians, corals, plants and fish but none of the estimated loss considered co-extinctions. Similarly, conservation strategies based on evolutionary history at risk generally rely on species IUCN threat status but do not account for the dependence of species on each other to survive (e.g. May-Collado and Agnarsson, 2011; Gudde et al., 2013; Jetz et al., 2014; Veron et al., 2017). Co-extinctions could be the primary fuel for the extinction crisis and particularly affect mutualistic communities (Rezende et al., 2007; Dunn et al., 2009). Mutualistic networks used to exhibit remarkable persistence and stability. However, current threats, including climate change, nutrient enrichment, habitat fragmentation, overhunting and exotic species introduction, have decreased the resilience of mutualistic communities and precipitated local extinctions (Tylianakis et al., 2008; Dunn et al., 2009; Kiers et al., 2010). Moreover, when conditions become more stressful, mutualist species may increasingly

73 depend on each other. They may thus collapse simultaneously when a critical point in the

74 driver of extinction has been reached (Dakos et al., 2014; Lever et al., 2014).

75   Plant-pollinator networks may be particularly vulnerable to such co-extinction

76 phenomena due to the global fall in pollinator populations (Potts et al., 2010; 2016). Declines

77 in pollinator species have been documented in highly industrialized countries due to

78 anthropogenic pressures, such as changes in land use, pesticides, management-induced

79 pathogens, and invasive species (Potts et al., 2016). Pollinator decline may be interdependent

80 with plant decline as a large proportion of plants depend on animal pollination for

81 reproduction (Ollerton et al., 2011). For example, in Britain and the Netherlands, Biesmeijer

82 et al. (2006) found evidence of a decline in bee diversity that corresponded to a parallel

83 decline in plant abundance. Co-extinctions are expected to weaken the sustainability of

84 mutualistic networks and cause loss of species richness (e.g., Memmott et al., 2004),

85 functional diversity (Sellmann et al., 2016) and evolutionary history (Dunn et al., 2009).

86 However, the magnitude of losses in these three components of biodiversity may differ (Dunn

87 et al., 2009; Cianciaruso et al., 2013; Sellmann et al., 2016). Here, we focus on the impacts of

88 co-extinctions on evolutionary history which have been poorly investigated so far.

89   It has been well established that the tree of life is vulnerable to co-extinctions when

90 interactions are evolutionarily conserved, i.e., when closely related species tend to share many

91 interacting partners (Gomez et al., 2010; Elias et al., 2013; Fontaine and Thébault 2015).

92 First, some species interact with partners sharing similar traits, which may be related to a

93 shared evolutionary history (Faith 1992; Thompson, 2005; Santamaría and Rodríguez-Gironés

94 2007; Junker et al., 2013; Chamberlain et al., 2014; but see Ives and Godfray, 2006; Fontaine

95 et al., 2009). Consequently, the extinction of those species can increase the vulnerability of

96 closely related partners. These extinctions may thus cause a fast decline in evolutionary

97 history (Rezende et al., 2007; Cianciaruso et al., 2013; Vieira et al., 2013). Second, the

phylogenies of interacting species may mirror each other, a hypothesis called "Fahrenholz's rule" (Fahrenholz, 1913). The extinction of related species may lead to the co-extinction of closely related interacting partners (Light and Hafner, 2008; Cruaud and Rasplus, 2016; but this still must be demonstrated in mutualistic networks).

Only a few studies have considered co-extinctions to estimate threatened evolutionary history, and the models used by these studies were too simplistic. For example, they assumed that a plant could go extinct only when all its interacting pollinators were lost (Rezende et al., 2007; Cianciaruso et al., 2013), or they did not account for the expected losses based on phylogenetic complementarities among species (Vieira et al., 2013; Vieira and Almeida-Neto, 2015). A complementarity approach based on extinction risks states that the probability that a deep branch will go extinct depends on the probability that all the species supported by the given branch go extinct (Faith, 2008). If complementarity is not accounted for, the risk of losing deep branches is incorrectly assessed, as is the risk of losing PD (Steel et al., 2007; Faith 2008; Veron et al., 2016). Here, we propose a new method to fill this gap and to estimate potential extinction risks in a phylogenetic context that accounts for the probabilities of co-extinctions and phylogenetic complementarities among species. We assessed how much evolutionary history could be lost when consecutive co-extinctions occur. This approach enabled us to identify species for which extinction would cause a disproportionate loss of evolutionary history in their interacting partners. We then investigated how the timing of extinctions as well as plant and pollinator features related to mutualism that may influence the risks of losing evolutionary history. We applied this approach to eight flower visitor networks in Europe. In spite of the previously mentioned benefits to use PD in conservation, concrete actions are scarce. The EDGE program (Isaac et al., 2017), the list of threatened fish in the U.S (Fay and Thomas, 1983), educational panels in the Australian museum of natural history (Faith, personal communication), are among the few practical examples we are aware of

123 (Veron et al., 2016). This may be because of practical difficulties, such as the lack of

124 phylogenies for some taxa or because the benefits to use evolutionary history in conservation

125 are misunderstood (Winter et al., 2012). We demonstrated, thanks to our concrete case study,

126 how evolutionary history and co-extinction can be incorporated in biodiversity loss

127 assessments to enlighten conservation actions. Our method has thus the potential to be a new

128 valuable contribution to design a framework for PD conservation.

129 ## 2. Materials and Methods
130

131 2.1 Expected loss of PD and species richness due to co-extinctions

132 The method we propose is based on the inclusion of probabilities of co-extinction in an index

133 of expected loss of PD (ExpPDloss).

134 *Expected loss of PD*

135 The ExpPDloss index has been highly recommended for measuring the PD of a group

136 threatened with extinction (plants in our case study). Indeed, this index accounts for the

137 phylogenetic complementarities of extinction risks among species of a given group (Steel et

138 al., 2007; Faith, 2008; Veron et al., 2016). Consider a phylogenetic tree, hereafter simply

139 named 'tree', for the group of species of interest (plants in our case study). The tips of the tree

140 represent species. Consider also a vector named 'proba' with the extinction probabilities of

141 these same species. Expected loss of PD (ExpPDloss) can be calculated as follows:

142

143 $$ExpPDloss(tree, proba) = \sum_{b} L_b \prod_{k_b} p_{k_b} \quad \text{(eq. 1)}$$

144 where k_b designates the kth descendant of branch b in tree, p_{k_b} is the extinction probability of

145 the kth descendant of branch b, and L_b is the length of branch b (Faith, 2008; Fig. 1).

146   We define the expected loss of species richness (ExpSRloss) as the sum of extinction

147   probabilities:

148    $$ExpSRloss(proba) = \sum_i p_i \text{ (eq. 2)}$$

149   where i designates the ith species (plant species in our study) and p_i denotes its extinction

150   probability.

151   In our model, we then used the probabilities of co-extinctions in eq. 1 and eq. 2.

152   *Probabilities of co-extinctions*

153   We defined the probabilities of co-extinctions following Vieira et al. (2013):

154    $P_{ij} = R_i d_{ij}$ (eq. 3)

155   where P_{ij} accounts for the co-extinction probability of the affiliate species i following the loss

156   of species j, R_i is the demographic dependence of species i on mutualism and d_{ij} is the

157   dependence of species i on species j. In plant visitation networks, we estimated R_i for each

158   plant species according to three reproduction traits: pollination vector, self-sterility and

159   reproduction type. The qualitative data for those traits were derived from the BioFlor database

160   (Klotz et al., 2002). We then converted the qualitative data for those three traits into discrete

161   quantitative scores (Table 1). R_i was then assessed as the mean value of the three scores. We

162   calculated d_{ij} as the proportion of interactions that species i loses when species j goes extinct

163   out of all interactions involving species i (Bascompte et al., 2006). The vector of co-extinction

164   probabilities due to the loss of pollinator j refers to the probabilities of co-extinctions of all

165   the plants that interact with species j (Fig. 1).

166   Include figure 1 and table 1

167   2.2 Loss of plant evolutionary history due to pollinator extinctions

168   *Consequences of pollinator extinctions for plant ExpPDloss and ExpSRloss*

169   We used data from eight plant visitation networks sampled in Europe to estimate the

170   possible consequences of pollinator extinctions for the plant evolutionary history under

171   various scenarios of species loss. Full descriptions of networks can be found in the literature

172   (Herrera et al., 1988; Elberling and Olesen, 1999; Memmott, 1999; Dicks et al., 2002;

173   Bartomeus et al., 2008; Dupont and Olesen, 2009) as well as in the Web of Life

174   database http://www.web-of-life.es. Four networks were binary, whereas the other four were

175   quantified with visitation frequencies. The approach we developed allows for the

176   manipulation of both types of matrices. In six networks, only the insects that were seen

177   touching plant reproductive organs were sampled, whereas in two networks, all visitors were

178   recorded. Here, we considered all insects recorded as potential pollinators.

179   We performed random sequences of pollinator species extinctions independently in each

180   network. As the order in which pollinator extinctions will occur is highly uncertain, we

181   performed 1000 random sequences of pollinator extinctions in each network. Each of those

182   sequences defined an extinction scenario from the first species to go extinct to the last. After

183   the extinction of a pollinator, we updated the *dij* (eq. 3) for each plant as its cumulative

184   number of interactions lost divided by its initial number of interactions (without extinctions)

185   and re-calculated the probabilities of co-extinction for each plant (P_{ij} in eq. 3). We used these

186   probabilities of co-extinction to successively update the ExpPDloss values (eq. 1) until all

187   pollinators were extinct. We then measured the variation in ExpPDloss caused by the

188   extinction of each pollinator. This measure, called EPL*j* for the extinction of pollinator *j*, is

189   thus:

190    $EPL_{j,k} = ExpPDloss_{[1,\pi jk]} - ExpPDloss_{[1,\pi jk-1]}$ (eq. 4)

191   where πjk is the position of the focal pollinator j in the kth extinction sequence.

192   ExpPDloss$_{[1,\pi jk]}$ is the cumulated ExpPDloss in plants caused by pollinator extinctions from

193   the 1st species to the focal species j, and ExpPDloss$_{[1,\ \pi jk-1]}$ is ExpPDloss when the first πjk-1

194   pollinators of extinction sequence k are driven to extinction. The sum of the values obtained

195   represented the cumulated loss of PD when several pollinators went extinct. Even if we

196   focused on PD loss, we also estimated the variation in SR loss caused by the extinction of

197   each pollinator:

198    $$ESRL_{j,k} = ExpSRloss_{[1,\pi jk]} - ExpSRloss_{[1,\pi jk-1]} \text{ (eq. 5)}$$

199   We then estimated the variation in ExpPDloss per lost interaction because the number of

200   interactions varies among pollinators and can affect the plant ExpPDloss following its

201   extinction:

202    $$EPLint_{j,k} = \frac{ExpPDloss_{[1,\pi jk]}}{INTloss_{[1,\pi jk]}} - \frac{ExpPDloss_{[1,\pi jk-1]}}{INTloss_{[1,\pi jk-1]}} \text{ (eq. 6)}$$

203   where INTloss$_{[1,\pi jk]}$ is the cumulative number of interactions lost to the focal species j when

204   the first species goes extinct in extinction sequence k; INTloss$_{[1,\pi jk-1]}$ is the cumulative number

205   of interactions lost when the first πjk-1 species are driven extinct in extinction sequence k.

206   EPLint$_{j,k}$ can be negative when INTloss increases faster than ExpPDloss.

207   We proposed five different metrics to estimate the expected consequences of co-extinctions

208   on evolutionary history over the 1000 simulated extinction sequences (Fig. 2):

209   -   The mean expected variation in plant PD caused by the loss of each pollinator species j

210   (eq. 4) over k sequences of extinctions

211    $$EPL_{j,mean} = \frac{1}{1000} \sum_{k=1}^{1000} EPL_{j,k}$$

9

212   - The mean expected variation in plant SR caused by the extinction of each pollinator

213   species j (eq. 5) over k sequences of extinctions

$$ESRL_{j,mean} = \frac{1}{1000} \sum_{k=1}^{1000} ESRL_{j,k}$$

214

215   - As mean losses may be highly dependent on the number of interactions lost, we

216   calculated the mean variation in plant PD per interaction lost (eq. 6) over k sequences of

217   extinctions

$$EPLint_{j,mean} = \frac{1}{1000} \sum_{k=1}^{1000} EPLint_{j,k}$$

218

219   - A measure that allows for the identification of species that cause high losses only when

220   they go extinct in a particular position in the sequence of pollinator extinctions. This is

221   calculated as the difference between the maximum and mean loss in plant PD caused by

222   the extinction of pollinator j over k sequences of extinctions

$$EPL_{j,max-mean} = max_{k=1}^{1000}(EPL_{j,k}) - EPL_{j,mean}$$

223

224   - In case a single extinction occurs, we estimated the ExpPDloss caused by pollinator j

225   when it goes extinct first, independent of which pollinators may be lost after its own

226   extinction

$$EPL_{j,unique} = ExpPDloss_j$$

227

228   where $ExpPDloss_j$ means the expected PD loss due to the loss of pollinator species j only.

229   We estimated those metrics for pollinators individually and then analysed the results by

230   species order using two-sided Wilcoxon tests.

231   Include figure 2

232   *Connecting pollinator and plant features with PD loss and SR loss*

233   Second, we looked for features related to interactions between plants and pollinators

234   and to plant evolutionary history that may explain why some pollinator extinctions are more

235   prone to cause high losses of plant PD and SR. Although some effects may be expected, we

236   aimed to disentangle which features had the highest influence on diversity loss.

237   *Pollinator and plant features* – As previously stated, phylogenetic conservatism is expected to

238   increase the loss of PD compared to a random distribution of interactions (Rezende et al.,

239   2007). Thus, for each pollinator, we estimated the phylogenetic signal of its interactions using

240   the D statistic from Fritz and Purvis (2010). We used the phylogenetic randomness test of the

241   D statistic, which tests if a trait is more conserved than if it was randomly shuffled relative to

242   the tips of the phylogeny (a p-value close to 1 means that the trait is more conserved than

243   random). However, this statistic measures the phylogenetic signal only for binary data. In

244   quantitative networks, we first measured the D statistic without considering the number of

245   visits and then used a second metric called evodiv, which allows for the inclusion of the

246   number of visits (high values of evodiv denote phylogenetic overdispersion, and low values

247   thus stand for phylogenetic clustering; Appendix A1). We then estimated pollinator

248   generalism as the number of interactions 'Nb' in the binary networks and by the Paired

249   Difference Index (PDI; Dormann, 2011) in quantitative networks, as recommended by Poisot

250   et al. (2012). Regarding plant features we estimated their evolutionary distinctiveness (ED

251   metric; Redding et al., 2006), generalism (defined as the number of interacting partners of a

252   plant or the PDI index in binary and quantitative networks, respectively), and dependence on

253   mutualism (R values). Then, for each pollinator we estimated the mean of those three features

254   over all its interacting plants, i.e. mean plant ED, mean plant generalism, and mean plant R.

255   *Statistical modelling* – To model the relationships between the loss of plant SR and PD and

256   pollinator and plant features, we used generalized linear mixed-effects models assuming a

257   negative binomial distribution. We ran one model for each possible combination of the tested

11

258   variables using the dredge function of the MuMIn R package version 1.9.13 (Barton, 2013).

259   The most complex model included the additive fixed effects of pollinator and interacting plant

260   features, i.e. phylogenetic overdispersion, pollinator generalism, mean plant ED, mean plant

261   generalism, mean plant R, and their pairwise interactions. All models included a 'network'

262   random effect. We then generated a set of best models, selected on the basis of Akaike's

263   Information Criteria (AIC; Burnham and Anderson, 2003; adjusted for small sample size, i.e.,

264   AICc). The lower the AICc, the better the model. The 'best model set' was defined as that for

265   which cumulative AICc weight (*w*, i.e., a measure of relative statistical support) reached 95%

266   of the total AICc weights. The parameter estimates were averaged across the selected models

267   using the model averaging function (full average; Barton, 2013). This procedure enabled us to

268   account for model selection uncertainty. We first centred and scaled the response variables in

269   each network, which enabled us to compare the relative strength of each effect, regardless of

270   their magnitude (mean and variance). We assessed the effects of plant traits, pollinator traits

271   and their interactions on diversity loss in all networks pooled together. All statistical analyses

272   were performed in R version 3.4.0 (R core team, 2017).

3. Results

273

274

275 3.1. Classification of pollinators according to expected loss of PD and SR

276   For each network, we provide data on how much additional plant diversity would be

277 lost after the extinction of each pollinator. We first compared species rankings in the different

278 measures of PD and SR loss presented in the methods. The highest correlations (Spearman's

279 test) were between the mean and unique loss of PD (cor = 0.95 and cor=0.88 in qualitative

280 and quantitative networks, respectively; Table 2) and between the mean loss of PD and SR

281 (cor = 0.88 and cor=0.82 in qualitative and quantitative networks, respectively; Table 2). In

282 contrast, the measure that identifies species that cause a high loss of PD only when they go

283   extinct in a particular position in the sequence of pollinator extinctions (EPL$_{\text{max-mean}}$) had the

284   lowest correlation with other measures (Table 2).

285   Include table 2

286   In qualitative networks, losses of PD and SR are generally similar between Coleoptera,

287   Hymenoptera and Diptera, whereas they are lower for Lepidoptera (Fig. 3). The individual

288   species that cause the highest loss in PD and SR are hymenopterans and dipterans. In

289   quantitative networks, the order in which losses are the highest varies with the measure

290   considered (Fig. 4). The mean and unique loss of PD caused by lepidopteran extinctions are

291   significantly lower than those when hymenopterans go extinct. The mean losses of PD per lost

292   interaction are lower in Coleoptera than in Diptera and Lepidoptera. In contrast, the maximal

293   losses minus the mean losses are higher in Coleoptera than in all other orders. Losses of SR

294   are lower in lepidopterans compared to coleopterans and hymenopterans (Fig .4). The loss of

295   plant diversity caused by individual pollinator extinctions can be found in Appendices A2-A9.

296   Include figures 2 and 3

297   3.2.Plant and pollinator features related to high diversity loss

298   We then looked at the relations between losses (measures EPL$_{\text{mean}}$, ESRL$_{\text{mean}}$,

299   EPLint$_{\text{mean}}$, EPL$_{\text{max-mean}}$ and EPL$_{\text{unique}}$) and plant and pollinator features using multi-model

300   selection based on AIC. The results are presented in Table 3. We found a low association

301   between features except between the number of pollinator interactions and the measure of

302   phylogenetic overdispersion "evodiv" (ρ= -0.55 in quantitative networks, Spearman

303   correlation). The effect of the phylogenetic signal may thus be better disentangled by the D

304   statistic than by the evodiv metric, even if the latter allows for the inclusion of the number of

305   visits. We found that variables that most explained the mean and unique expected loss of PD

306   ($\Sigma w_i=1$; measures EPL$_{\text{mean}}$ and EPL$_{\text{unique}}$) were pollinator generalism (significant positive

307 effect in qualitative networks), plant evolutionary distinctiveness (significant positive effect),

308 interaction overdispersion (negative effect) and plant generalism (significant negative effect)

309 (Table 3). We sometimes found a significant effect of the interaction between pollinator

310 generalism and plant evolutionary distinctiveness: generalist species pollinating evolutionarily

311 distinct plants may increase the mean and unique PD loss. However, pollinator generalism

312 had little effect in quantitative networks (Table 3b), probably because plant diversity losses in

313 those networks were more related to the number of lost interactions (measured as the number

314 of visits) rather than to the number of pollinators lost. As for the effect of interaction

315 overdispersion, this result may be due to its correlation with pollinator generalism (cor=-0.55

316 in quantitative networks). We found that the effect of phylogenetic signal, estimated using the

317 D statistic, was generally lower than for all other variables (Σw_i between 0.48 and 0.86). The

318 mean expected loss of PD per interaction lost ($EPLint_{mean}$) was driven by evolutionary

319 distinctiveness (positive effect) and plant generalism (negative effect). However, contrary to

320 the mean and unique loss of PD (EPL_{mean} and EPL_{unique}), we found a negative effect of

321 pollinator generalism in qualitative networks (Table 3a), meaning that extinctions of specialist

322 species would cause the highest loss in those networks. We also found a significant effect of

323 the interaction between plant and pollinator generalism such that extinctions of specialist

324 species pollinating specialist plants may cause a high mean expected PD loss per lost

325 interaction. The species causing high PD loss only when they go extinct in a particular order

326 in the sequence of extinction ($EPL_{max-mean}$) are specialist pollinators in qualitative networks

327 (Table 3a) and pollinators interacting with plants highly dependent on mutualism in

328 quantitative networks (Table 3b). Finally, the strongest effects we detected for the mean

329 expected loss of species richness ($ESRL_{mean}$) were pollinator and plant generalism (positive

330 and negative effects, respectively). Plant dependence on mutualism was present in most of the

331 selected models, but its effect was generally lower than for other variables.

4. Discussion

In this study, we investigated the potential consequences of co-extinctions on the loss of evolutionary history. Indeed, because of co-extinctions, the PD at risk could be higher than assessed from the probabilities of extinction alone. We thus developed a new method which accounts for the dependence of species on each other in a mutualistic network, the demographic dependence of species on mutualism and the phylogenetic complementarities among species. We identified several measures to estimate the risks of losing PD. First, we measured how much PD would be lost in the network when a single extinction occurs, this may enable the identification of pollinators for which primary extinction is expected to cause the highest PD loss. However, more than one species could be vulnerable to several extinction events (Dunn et al., 2009). As the order of pollinator extinctions in nature is usually unknown, for each species in each network, we estimated the average loss of plant diversity its extinction would cause regardless of its position in a sequence of extinction. However, some species co-extinctions cause relatively low losses of diversity on average, but this may disguise a potentially high impact when their extinction occurs in a particular position in the sequence of extinction. Some species may capture little unique evolutionary history, i.e., the last branch from which they descend is short, but they may also share deep and possibly long branches with other species. Depending on the sequence of extinction, these species can become the last survivors supporting those long branches. This reveals that PD can suddenly collapse once a number of co-extinction events occur. Finally, we estimated the expected loss of diversity per lost interaction following species extinctions. This determines which species extinctions would result in high PD losses independent of the number of interactions lost. This measure could identify specialist species for which extinction would cause the loss of a single evolutionary distinct plant.

357   Previous studies showed that high losses of PD following co-extinctions were mainly

358   due to a phylogenetic signal in the interactions (Rezende et al., 2007; Vieira et al., 2013;

359   Cianciaruso et al., 2013). Here, we showed that the variation in expected losses of PD due to

360   co-extinctions may be related to several combinations of factors, including high mutualism

361   dependency, plant and pollinator generalism, high evolutionary distinctiveness and/or

362   phylogenetic overdispersion of interactions. Plants that are highly dependent on mutualism

363   are expected to become more vulnerable when their pollinators are lost, increasing the risks of

364   losing both species and PD. However, we found that plant dependence on mutualism, despite

365   its positive effect, had a lower effect on PD loss and SR loss than other plant and pollinator

366   features. This is most likely because plants that are highly dependent on mutualism have

367   developed a strategy to avoid co-extinction: they tend to have a high number of partners to

368   compensate for the potential loss of a pollinator (Fricke et al., 2017). Indeed, we found that

369   plant generalism tends to decrease the consequences of pollinator co-extinctions for plant

370   diversity. A generalist plant that loses one of its interactions may still have a high number of

371   pollinators for its reproduction and dispersion, whereas this may not be the case for a

372   specialist. Thus, plant generalists tend to show a lower increase in their probability of co-

373   extinction than specialists following the extinction of pollinators. In contrast, we found that

374   pollinator generalism had a strong effect on the expected loss of PD and SR in all the metrics

375   we measured except for the mean loss of PD per lost interaction. Indeed, when a generalist

376   pollinator became extinct, it increased the probability of co-extinctions for a relatively high

377   number of plants, directly increasing the SR and PD at risk. High expected PD losses

378   following co-extinction events were also due to the evolutionary distinctiveness of species.

379   The extinction of a species interacting with a partner isolated in a phylogeny and descending

380   from a long branch is expected to increase the risks of losing this unique evolutionary history.

381   The loss of evolutionary distinctiveness has been shown to be the driver of high PD losses but

382   has rarely been examined in a co-extinction context (Veron et al., 2016). We found that

383   phylogenetic signal, which was estimated using the D statistic, had little effect on the

384   expected PD loss. Even if closely related plants lose some of their interactions, the risks of

385   losing their shared branches, and thus of causing high PD losses, may still be low if those

386   species still have many interactions or/and if their dependency on mutualism is low. We also

387   used a second metric, evodiv, which assesses interaction overdispersion in a phylogenyand

388   enables the inclusion of the frequency of visits per species and giving a score to species with

389   only one interaction (Appendix A1). We found that interaction overdispersion may decrease

390   the risks of losing PD (Table 3). However, effect of the evodiv measure on PD loss may be

391   due to its correlation with pollinator generalism. We also found that some factors significantly

392   interacted with each other (Table 3). The interaction of the extinction of generalist pollinators

393   with evolutionarily distinct plants in particular may cause a high mean expected loss of PD

394   (EPL_{mean}), whereas specialist pollinators interacting with specialist plants may result in a high

395   mean loss of PD per lost interaction ($EPLint_{mean}$). However, an area for future research would

396   be to investigate how functional traits of pollinators, such as traits related to habitat

397   specificity, dispersal or reproduction, may influence co-extinction events. This may help to

398   understand the loss of diversity due to co-extinctions in a broader context than a local

399   mutualistic network.

400   A probabilistic model implies that a species has a risk of going co-extinct even if some

401   of its interactions remain, and this risk increases when more interactions are lost (Vieira et al.,

402   2013; Vieira and Almeida-Neto, 2015; Vanbergen et al., 2017). We also considered the

403   principle of the phylogenetic complementarity of extinction risks by measuring an index of

404   expected loss of PD that has been highly recommended but rarely employed (Faith, 2008;

405   Veron et al., 2016). The phylogenetic complementarity of extinction risks represents the fact

406   that the risk of losing a deep branch depends on the probabilities of extinctions of all the

407   species it supports. Our model thus improves the few existing models of diversity loss in

408   interaction networks by applying this principle to co-extinction events. However, additional

409   factors of extinction risks in mutualistic networks could be considered. Mutualistic networks

410   may be especially resilient to species loss (Timóteo et al., 2016). Plants may compensate for

411   pollination failure by interacting with new partners when some pollinators are lost. Indeed, as

412   observed in New Zealand (Pattemore and Wilcox, 2011), the loss of some pollinators may

413   result in a greater availability of resources for other pollinators. Plants can then be pollinated

414   by novel species, or their interactions with their remaining partners can become more

415   frequent. Our approach assumed no compensation even if the R variable gives some

416   information about whether a plant may propagate or reproduce owing to non-insect species or

417   to a physical factor. Despite possible compensation, the loss of a single pollinator could in

418   fact make all plants in the community more vulnerable due to changes in interspecific

419   competition between pollinators. Brosi and Briggs (2013) showed that the loss of a single

420   pollinator could reduce floral fidelity, resulting in the reduction of pollination functioning and

421   plant reproduction functions and thus a decline in plant abundance. Competition could thus be

422   an additional factor to consider in co-extinction models.

423   We did not consider the impacts of higher-order extinctions, i.e., that the increase in the

424   probability of plant extinction due to the extinction of a single pollinator may also increase the

425   probability of extinctions of other pollinators interacting with this plant, again increasing

426   probability of extinctions of plants, and so on. Indeed, a higher probability of extinctions in

427   plants may be reflected in a lower floral availability for pollinators causing their parallel

428   decline (Potts et al. 2010). Our estimations are thus conservative. Indeed they, do not account

429   for pollinator probabilities of extinctions and thus probably underestimate the true expected

430   loss of evolutionary history. The effect of this possible vortex of extinction remains to be

431   investigated. Including higher-order extinctions could also help to estimate possible sequences

432   of pollinator extinctions based on their probability of higher-order extinctions or to estimate

433   the expected loss of pollinator SR and PD. Instead, we chose to focus on the direct impact of

434   co-extinctions on expected PD loss and SR loss. Indeed, it is unclear how the increase in plant

435   extinction probability may influence the pollinator probability of extinction. Knowledge and

436   data on how to estimate the pollinator dependency on mutualism, i.e., R values for pollinators

437   (e.g., Vanbergen et al., 2017), are still lacking. Considering direct co-extinction events may

438   also help better disentangle which pollinator and plant features result in high risks of losing

439   PD and SR.

440   Although further research is needed to apply our approach over a large range of

441   datasets accounting for the spatio-temporal dynamics of networks, our case study provides an

442   overview of the potential of this method. Our approach will allow researchers to tackle

443   various conservation issues by examining the impacts of co-extinctions on PD, the associated

444   loss in functional diversity and in benefits for society (Faith et al., 2010), including the

445   following: *i)* identifying species for which extinction would cause, on average, a

446   disproportionate loss of evolutionary history in interacting groups; *ii)* identifying when PD

447   should collapse due to the co-extinctions of the last species supporting deep branches; *iii)*

448   assessing the loss of evolutionary history caused by the co-extinctions of a species or of a

449   group of species and guiding prioritization for conservation (e.g., yellow-faced bees in Hawaii

450   became the first protected pollinators in the U.S.); *iv)* combining information on threat status

451   and co-extinction probabilities to assess expected losses of diversity and better define the

452   sequence of pollinator extinctions. Indeed, when more data on pollinators' extinction risks

453   (threat status) are available, an association between our model and an expected sequence of

454   pollinator extinctions could reveal which extinction scenarios are more likely to happen. For

455   example, despite numerous data-deficient and non-assessed species, the European Red Lists

456   for bees (Nieto et al., 2014), butterflies (Nieto et al., 2010) and beetles (Van Swaay et al.,

457   2011) have recently been published. An interesting prospect would be to assess the Red List

458   of flies as they are among the species that carry out the most pollination services (Orford et

459   al., 2015). New long-term monitoring schemes are also needed to make such Red Lists

460   possible.

461   We estimated the expected losses of PD in plant visitation networks due to the high

462   level of threats faced by pollinators that may cause a parallel decline in plants (Biesmeijer et

463   al., 2006; Regan et al., 2015). However, our approach is very flexible, can be applied to many

464   types of interaction networks and can be easily adapted to diversity measures such as the

465   expected loss of functional diversity (Faith, 2015). An especially crucial issue for

466   conservation would be to assess the impacts of co-extinctions on the PD of non-visible and

467   less charismatic taxa. Indeed, such taxa represent a great amount of evolutionary history, and

468   the main threat they face may be the decline of their hosts (Trewick and Morgan-Richards,

469   2016). In this context, we encourage future research in host-parasite networks as the impacts

470   of co-extinctions may be particularly severe in parasitic interactions (Dunn et al., 2009; Dallas

471   and Cornelius, 2015; Farrell et al., 2015; Strona, 2015).

472

473

474   # 4 Conclusion

475

476   Co-extinctions have scarcely been accounted for in estimating losses in diversity and

477   especially PD. However, co-extinctions are likely to result in higher losses of diversity than

478   expected. Here, we defined a new model to assess the expected loss of PD that integrates the

479   probabilities of co-extinctions and the phylogenetic complementarities among species.

480   Testing our method on plant-pollinator networks, we showed how co-extinctions could prune

481   the tree of life depending on the order of pollinator extinctions. We showed that losses of PD

due to co-extinctions could increase mainly because of pollinator generalism, plant specialism

and plant evolutionary distinctiveness. Contrary to our expectations, we found only a low

effect of phylogenetic signal and plant dependence on mutualism. We thus recommend the

use of our approach to generate more accurate assessments of at-risk PD by integrating the

probabilities of co-extinctions and species phylogenetic complementarity.

5 Acknowledgments

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693 Tables

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695 **Table 1**. Qualitative and quantitative values for plant reproduction traits used to assess plant

696 dependence on mutualism (R).

Reproduction trait	Qualitative value	Quantitative value
Type of reproduction	by seed	1
	mostly by seed	0.75
	by seed and vegetatively	0.5
	mostly vegetatively	0.25
	vegetatively	0
Self-sterility	self compatible	0
	frequently self compatible	0.3
	frequently self incompatible	0.6
	self incompatible	1
Pollination vector	insects-the rule	1
	insects-always	0.8
	insect-often	0.6
	insect-possible	0.4
	insects-rare	0.2
	other vector than insects	0

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699 **Table 2**

700 Spearman correlation tests between the different measures of diversity loss due to co-

701 extinctions in a) qualitative networks b) quantitative networks

a)	$EPLinter_{mean}$	$ESRL_{mean}$	$EPL_{max\text{-}mean}$	EPL_{unique}
EPL_{mean}	0.61	0.88	0.18	0.95
$EPLinter_{mean}$		0.36	0.07	0.65
$ESRL_{mean}$			0.21	0.77
$EPL_{max\text{-}mean}$				0.13

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b)	$EPLinter_{mean}$	$ESRL_{mean}$	$EPL_{max\text{-}mean}$	EPL_{unique}
EPL_{mean}	0.25	0.82	0.06	0.92
$EPLinter_{mean}$		0.13	-0.16	0.30
$ESRL_{mean}$			0.08	0.83
$EPL_{max\text{-}mean}$				-0.01

Figure legends

Fig. 1. (double column) Practical example for the calculation of expected loss of phylogenetic diversity and species diversity due to co-extinctions.

The figure represents a mutualistic network of four pollinators and nine plant species as well as the plant phylogeny. Indices are calculated following the loss of the pollinator D. Branch lengths are shown as well as branch lengths (in red) weighted by the probability of co-extinctions (R in blue and d in red) and following the loss of species D.
 The expected loss in plant species richness following the extinction of pollinator D, noted $ExpSRloss_D$, is equal to $d_{7D}*R_{7D} + d_{8D}*R_{8D} + d_{9D}*R_9 = 1.25$ and the ExpSRloss per interaction following the extinction of species D is equal to $ExpSRloss_D$/Number of interactions lost by the extinction of $D = 1.25/3 = 0.41$. The expected loss of phylogenetic diversity following the loss of pollinator D is then calculated as follow: $ExpPDloss_D = 10$ My*1*0.3*0.5 + 65 My*1*0.3*0.5*0.7 + 10 My*1*0.7 + 85 My*1*0.5 = 57.8My. Then, ExpPDloss per interaction = 57.8/3 = 19.2My.

Fig. 2. This figure represents interactions in a mutualistic network (Dicks et al., 2002) and five measures of diversity losses following individual pollinator extinctions: EPLmean, $ESRL_{mean}$, $EPLint_{mean}$, $EPL_{max\text{-}mean}$ and EPL_{unique}. Each histogram represents the mean and standard deviation (when existing) of those five measures. In the interaction network, pollinators are found on the upper side of the graph (red colored bars) and plants on the lower side (green cored bars). The width of the bars represents the number of interactions of a species. Similar figures for each network can be found in appendices A2-A9.

Fig. 3. Loss of plant diversity due to co-extinctions in each pollinator Orders in qualitative networks. Results were centred and scaled. We did not represent Orders represented by few species (e.g. Hemiptera). We did not represent species whose Order was unknown. The two species of each Order whose co-extinctions would cause the highest plant diversity loss are plotted on the graphics. Results of two-sided Wilcoxon tests comparing diversity losses between Orders are represented by symbols "a", "b" and "ab". When symbols are "a", "a" and "b" Orders which have been attributed a "a" cause similar diversity losses whereas the Order which has been attributed a "b" is significantly different from the "a" groups in term of

738 diversity loss; When values are "a", "b", and "ab", Orders with "a" and "b" are significantly
739 different whereas the Order "ab" is not significantly different from both "a" and "b".

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741 **Fig. 4.** Loss of plant diversity due to co-extinctions in each pollinator Orders in quantitative
742 networks. Results were centred and scaled. We did not represent Orders represented by few
743 species (e.g. Hemiptera). We did not represent species whose Order was unknown. The two
744 species of each Order whose co-extinctions would cause the highest plant diversity loss are
745 plotted on the graphics. Results of two-sided Wilcoxon tests comparing diversity losses
746 between Orders are represented by symbols "a", "b" and "ab". When symbols are "a", "a" and
747 "b" Orders which have been attributed a "a" cause similar diversity losses whereas the Order
748 which has been attributed a "b" is significantly different from the "a" groups in term of
749 diversity loss; When values are "a", "b", and "ab", Orders with "a" and "b" are significantly
750 different whereas the Order "ab" is not significantly different from both "a" and "b".

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753 Appendices
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755 Measure of phylogenetic over-dispersion (Appendix A1); Expected loss of plant phylogenetic
756 diversity and species richness due to co-extinctions in 8 plant visitor networks for different
757 conservation strategies are available online (Appendix A2-A9). The authors are solely
758 responsible for the content and functionality of these materials. Queries (other than absence of
759 the material) should be directed to the corresponding author.