Phylogenetic diversity of plants alters the effect of species richness on invertebrate herbivory

Long-standing ecological theory proposes that diverse communities of plants should experience a decrease in herbivory. Yet previous empirical examinations of this hypothesis have revealed that plant species richness increases herbivory in just as many systems as it decreases it. In this study, I ask whether more insight into the role of plant diversity in promoting or suppressing herbivory can be gained by incorporating information about the evolutionary history of species in a community. In an old field system in southern Ontario, I surveyed communities of plants and measured levels of leaf damage on 27 species in 38 plots. I calculated a measure of phylogenetic diversity (PSE) that encapsulates information about the amount of evolutionary history represented in each of the plots and looked for a relationship between levels of herbivory and both species richness and phylogenetic diversity using a generalized linear mixed model (GLMM) that could account for variation in herbivory levels between species. I found that species richness was positively associated with herbivore damage at the plot-level, in keeping with the results from several other recent studies on this question. On the other hand, phylogenetic diversity was associated with decreased herbivory. Importantly, there was also an interaction between species richness and phylogenetic diversity, such that plots with the highest levels of herbivory were plots which had many species but only if those species tended to be closely related to one another. I propose that these results are the consequence of interactions with herbivores whose diets are phylogenetically specialized (for which I introduce the term cladophage), and how phylogenetic diversity may alter their realized host ranges. These results suggest that incorporating a phylogenetic perspective can add valuable additional insight into the role of plant diversity in explaining or predicting levels of herbivory at a whole-community scale.

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Introduction

The insect herbivore flies, crawls, hovers, and feeds in a matrix of stems, roots, flowers and leaves. Thousands do this in a typical community of plants in what – to us – is an impenetrably complex tangle of traits, each the product of millions of years of evolution. How then are we to understand the aggregate patterns that emerge from such a community? Indeed, community ecologists have long struggled to understand how the identity and traits of individual plant species add together and interact to determine herbivore communities and the damage they cause.

Though much work on insect herbivory has focused on interactions between single pairs of insect and plant species, it is also important to understand the phenomenon at the level of whole plant communities. After all, many of the consequences of major ecosystem changes will be manifest at the level of the community, and one-to-one interactions may not always be additive (Agrawal, Lau, & Hamback 2006; Agrawal *et al.* 2007).

One way of understanding herbivory at the community level is to look at the effects of plant species richness. Plant species richness is one of the simplest way to summarize information about many species at the community level, and studies of its role in herbivory link up nicely with the body of literature on the relationship between diversity and ecosystem functioning (Siemann *et al.* 1998; Haddad *et al.* 2001; Loreau *et al.* 2001; Hooper *et al.* 2005; Cardinale *et al.* 2006; Balvanera *et al.* 2006; Cardinale *et al.* 2007; Scherber *et al.* 2010a). Insect herbivore damage is a useful reflection of the activities of insect herbivores in plant communities, as well as a phenomenon of interest in and of itself, with implications for the health of a plant community.

There are some clear theoretical predictions about the effects of plant species richness on herbivory, which derive from a simple understanding of direct trophic interactions between plants and insects. Root (1973) suggested that increased plant species richness should lead to a decrease in specialist herbivores, and thus to a decrease in herbivory. The Resource Concentration Hypothesis states that if the number of plant species in a patch is higher, the density of each plant species must be lower, and so specialist herbivores of those species will be less likely to find such a patch, stay in such a patch, and do damage in such a patch. On the other hand, the presence of a wide variety of plant species provides a wide variety of nutritional resources for generalist herbivores, which may prefer to eat in diverse patches, and may thrive more in them too (Unsicker *et al.* 2008; Schuldt & Baruffol 2010). I will refer to this idea as the Dietary Mixing Hypothesis (after Bernays et al. 1994).

Unfortunately, previous empirical literature has not provided a clear picture of which

67   of these two hypotheses applies more widely to plant-herbivore systems, because whether

68   plant species richness has a positive, negative, or no relationship with herbivory depends on

69   the system under study. A review of the literature shows that there are roughly equal numbers

70   of studies showing that plant diversity has a positive effect on herbivory as there are showing

71   a negative effect, at least for studies that looked at the effect of species richness on the

72   magnitude of herbivory (Table 1). This suggests that the role of plant species richness may

73   sensitively depend on aspects of either the plant or the herbivore community. Based on the

74   Resource Concentration Hypothesis and the Dietary Mixing Hypothesis described above, the

75   relative abundance of generalist vs. specialist herbivores likely plays a role. For example, Lau

76   et al. (2008) were able to separate damage done by specialists and damage done by

77   generalists on *Lespedeza capita* planted in low and high diversity plots. They found that

78   damage by generalists increased with high plant diversity and that damage from specialists

79   decreased with high plant diversity, in accordance with the predictions of the Dietary Mixing

80   hypothesis and the Resource Concentration Hypothesis, respectively.

81   Species richness is only a coarse measure of the diversity and structure of a

82   community, and so including other sources of information about communities may help to

83   clarify such simple predictions. Attempts to include more of the natural complexity of plant

84   communities to understand community herbivory include using functional diversity in

85   addition to plant species richness (Siemann *et al.* 1998; Koricheva *et al.* 2000;

86   Prieur-Richard, Lavorel, & Linhart 2002; Scherber *et al.* 2006, 2010b) reducing species

87   composition to low dimensional quantitative measures using ordination (Koricheva *et al.*

88   2000; Pfisterer, Diemer, & Schmid 2003; Schaffers *et al.* 2008), and incorporating

89   information about plant species' evolutionary history, using community phylogenetics. Here, I

90   explore the use of community phylogenetics to understand insect herbivory at the plant

91   community level.

92   The increasing availability of phylogenetic information on plants and the recent

93   development of sophisticated ways of incorporating this information into diversity measures

94   (Helmus *et al.* 2007; Cavender-Bares *et al.* 2009; Vamosi *et al.* 2009; Cadotte *et al.* 2010;

95   Pausas & Verdú 2010), is opening a new avenue of exploration for understanding the effects

96   of plants on ecosystem function at the whole community scale. For example, recent analyses

97   have shown that various measures of phylogenetic diversity are associated with the

98   productivity of plant communities (Cadotte, Cardinale, & Oakley 2008; Cadotte *et al.* 2009;

99   Connolly *et al.* 2011; Flynn *et al.* 2011) and the insect assemblages associated with them

100   (Dinnage et al. 2012). Here, I show that incorporating phylogenetic diversity into hypotheses

101 about herbivory can provide a useful framework for predicting when species richness may

102 increase or decrease herbivory in plant communities.

103 Phylogenetic diversity may be particularly important to herbivores and herbivory

104 because of the widespread occurrence of herbivores with phylogenetically restricted diets –

105 they feed on a group of closely related species (Ehrlich & Raven 1964; Janzen 1980;

106 Ødegaard, Diserud, & Østbye 2005; Weiblen *et al.* 2006; Gossner *et al.* 2009; Futuyma &

107 Agrawal 2009). I will refer to these species as cladophages, from the greek *klados* for

108 'branch', and the greek *phagein* for 'to eat' – thus 'branch-eater', or an organism that feeds

109 preferentially on just one of the branches of the tree of life that is available to them. The act

110 of feeding in this manner can be called cladophagy. Ultimately, because many plant traits are

111 conserved through evolutionary time, phylogeny will often be a reasonable proxy for

112 phenotypic divergence – and thus phylogenetic diversity a reasonable proxy for phenotypic

113 diversity (Cavendar-Bares et al. 2009). Since herbivores are presumed to feed on

114 phenotypically similar plant species more often than not, phylogenetic diversity will

115 indirectly effect how herbivores interact with plant communities.

116 In this study I asked whether the phylogenetic diversity of old-field plant communities

117 can predict the amount of herbivore damage on plants at a community-scale.

118

119 **Materials and methods**

120 *Data collection*

121 The study was conducted at the Koffler Scientific Reserve (KSR) at Joker's Hill (King

122 City, Ontario, Canada; http://www.ksr.utoronto.ca/jh.html), a 350 hectare property containing

123 a mix of primary forest, secondary forest and open habitats, including a large area of old field

124 sites. I was granted permission by the site director – Ann Zimmerman – to conduct the

125 research there.

126

127 *Species survey*

128 I haphazardly selected 38 10 x 10 meter plots spread across the available old field

129 habitat at KSR. In early August, I surveyed each plot within 4 randomly placed 1x1 meter

130 quadrats, one in each of the four quadrants of the larger plot. I noted the presence or absence

131 of each forb species within the quadrats and combined the data from all four quadrats into a

132 low resolution measure of abundance (ranging from 0-4) for each species within each 10x10

133 meter plot. I decided to focus on forbs to the exclusion of grasses for several reasons.

134 Herbivory from chewing insect is difficult to measure on grasses but is obvious on forbs.

135   There were only two common species of grass, which occurred in nearly every one of the

136   plots surveyed, and so inclusion of grasses in the phylogenetic diversity measures would have

137   only diluted the signal from the forbs. I hypothesized that phylogenetic diversity amongst

138   forbs would be the most important to understanding herbivory on forbs. This is because

139   grasses and forbs share few herbivores, except for the most generalist. As an example,

140   Dinnage et al. (2012) showed that the largest difference in arthropod communities collected

141   from different prairie plant species was between grasses and forbs.

142   Using this data, I calculated the species richness and abundance-weighted

143   phylogenetic diversity for all 38 plots. This data, along with the species composition of all 38

144   plots, can be found in Table S1 in Supporting Information.

145

146   *Herbivory survey*

147   In order to quantify the amount of herbivore damage in the plots, I selected 27 of the

148   most common species at KSR to measure damage (Fig. 1). These species acted as

149   phytometers to capture the overall herbivore pressure in the plot. In late August – over a

150   period of approximately two weeks – I measured herbivore damage rates in the 38 plots. For

151   each of the phytometer species that occured in a given plot, I sampled 10 individual plants by

152   counting the number of damaged leaves and the number of total leaves on each one. The

153   dataset then consisted of 1862 datapoints, each from an individual plant.

154   I chose this set of phytometer species before the commencement of the study, based

155   on my personal knowledge of which species seemed to make up the most apparent

156   membership of the old field communities (i.e. the 'overstory'). This intuition seems justified,

157   because of the 25 species which were surveyed in the plots, but for which I did not measure

158   damage, 17 were found in only 1 or 2 plots (<5% of total plots), and 24 were found in 5 or

159   fewer plots (<13% of total plots). It is unlikely that measurements of herbivory on these

160   species could have changed the results presented here substantially, unless rare species

161   systematically differed in their response to plant diversity. The one exception to this general

162   pattern was *Taraxacum officianale*, which was found in 16 plots and was not measured for

163   herbivory. However, *T. officianale* is an understory plant, which remains as a rosette for most

164   of its life history. It only produces a few leaves (4-10), all of which usually sustain some

165   herbivore damage (personal observation). Given this lack of variation in herbivory within *T.*

166   *offianale* under the method of measurement that I chose, it would be unlikely to affect the

167   results substantially (because if there is no variation, then it cannot vary with plant diversity

168   or anything else). For full information on species abundances across the 38 plots, see

169   Supplementary Table S1.

170

171   *Phylogeny and diversity indices*

172   I created a phylogenetic tree containing all the most common old field species found

173   at my site using methods previously described (Dinnage 2009). I then pruned the tree so that

174   the remaining species matched those found in the plots used for this study (Fig. 1).

175   Using this phylogeny I calculated an index of abundance-weighted phylogenetic

176   diversity for each plot. There are several such indices available – I chose Phylogenetic

177   Species Evenness (PSE; Helmus et al. 2007). PSE measures the amount of evolutionary

178   history represented in a community by calculating the expected variance in a hypothetical

179   continuous trait modeled as evolving through Brownian motion across the community

180   phylogeny, and is standardized by the expected variance of the same modeled trait on a star

181   phylogeny – where phylogenetic distances among all species are equal. This captures one of

182   the fundamental features of interest in phylogenetic diversity, that it may encapsulate

183   information about the ecological similarity of species in a community. I chose PSE for this

184   reason, and because it is theoretically (and empirically in this study) independent of species

185   richness. Thus, by using it, I could evaluate the *independent* contributions of species richness

186   and phylogenetic diversity without the problems of co-linearity and heteroscedasticity

187   common to many other phylogenetic diversity indices (e.g. Schweiger et al. 2008; Pio et al.

188   2011). PSE ranges between 0 and 1, where high values are associated with high phylogenetic

189   diversity. Low values are associated with low phylogenetic diversity, or phylogenetic

190   clustering – small average phylogenetic distances among species in the community. It is

191   possible that I could have seen different results with a different metric, but PSE is highly

192   correlated with a number of other metrics (Cadotte et al. 2010), and so the results presented

193   here should at least apply to this general 'class' of phylogenetic diversity indices.

194   I used species richness rather than an abundance-weighted measure because I was

195   interested in the effects of adding or subtracting species. This combined with the

196   phylogenetic diversity measure can give a statistical measure of adding species of different

197   phylogenetic distances from the species already present. In addition, abundance weighting is

198   easily interpretable for a measure like phylogenetic diversity, because in essence it is a

199   weighted average, and phylogeny is made from continuous measures of branch length. On the

200   other hand, abundance weighted measures like the Shannon-Weaver index are abstracted

201   quantities with no simple interpretation biologically (e.g. Goodman 1975; Austin 1999). I did

202   calculate evenness for the plots and it was not correlated with phylogenetic diversity, and so

203 the phylogenetic diversity measure, though abundance-weighted, was not confounded with

204 species evenness. In addition, evenness was not a significant predictor of herbivory when

205 included as a factor in the model described below, and so I did not use it.

206

207 *Statistical analysis*

208   In order to account for variation in species composition across plots, I used a

209 generalized linear mixed model (GLMM) with crossed random effects, to disentangle species

210 and plot-level effects on herbivory. The number of damaged leaves on a plant can be

211 modelled as a binomial distribution, with a damaged leaf considered a Bernoulli success (for

212 the herbivores) and an undamaged leaf a failure. Factors that may influence the probability of

213 a leaf being damaged were incorporated into the model with a logit link.

214   I used a logit-normal-binomial statistical model to analyze the data, as follows:

215

$$Damaged_i \sim Binomial(p_i, N_i)$$

$$Logit(p_i) = \alpha + \mu^1_{species[i]} + \mu^2_{plot[i]} + \mu^3_{obs[i]} + \beta_{pd}PD_{plot[i]} + \beta_{sr}SR_{plot[i]} + \beta_{pd*sr}(PD*SR)_{plot[i]}$$

$$+\beta_{date}DATE_{plot[i]}$$

$$\mu^1_{species[i]} \sim Normal(0, \sigma^2_{species}), \ \mu^2_{plot[i]} \sim Normal(0, \sigma^2_{plot}), \ \mu^3_{obs[i]} \sim Normal(0, \sigma^2_{obs})$$

220

221 Where $Damaged_i$ is the number of damaged leaves on individual plant i, p_i is the probability

222 of any given leaf on plant i being damaged, and N_i is the total number of leaves on plant i.

223 $PD_{plot[i]}$ and $SR_{plot[i]}$ are the phylogenetic diversity and the species richness, respectively, for

224 the plot in which plant i was found. $DATE_{plot[i]}$ is the date on which I sampled the plot, to

225 control for any increases in herbivory that may have occurred while the sampling was

226 ongoing. $\mu^1_{species[i]}$ and $\mu^2_{plot[i]}$ are the random effects for species and plot, respectively. $\mu^3_{obs[i]}$ is a

227 random effect for the individual observation which was included to account for any over- or

228 under-dispersion in the data since the binomial distribution contains no variance parameter.

229 The α (intercept) and β parameters are the fixed effects.

230   I used the lme4 package (Bates, Maechler, & Bolker 2011) for R statistical

231 environment (R Development Core Team 2010) to fit the model.

232   Plot level herbivory (after accounting for species-level variation, sampling date, and

233 observation) can then be estimated as the best linear unbiased predictors (BLUPs) –

234 sometimes referred to as the conditional modes – of p_i (hereafter estimated proportional leaf

235 damage). For plot j, this is equal to $p_j = Logit^{-1}(\alpha + \mu^2_j + \beta_{pd}PD_j + \beta_{sr}SR_j + \beta_{pd*sr}(PD*SR)_j)$.

236 Likewise, herbivory of species k (after accounting for plot-level variation, sampling date and

237 observation) is pk = $Logit^{-1}(\alpha + \mu^3_k)$. These values were used for plotting (Figs 2 and 3).

238 All continuous predictor variables were centred by subtracting their means prior to

239 analysis, so that the main effect of the variable refers to its slope at the mean of all other

240 variables.

241 Significance of the relationships between estimated proportional leaf damage and the

242 fixed factors was determined using a parametric bootstrap approach. For each fixed factor,

243 data was simulated under a simplified model without the fixed factor of interest. The full

244 model was then fit to the simulated data and the z statistic was calculated. The observed z

245 statistic from the full model was then compared to the distribution of z values obtained from

246 1000 such simulations, and a p value determined as the percent of simulated z values whose

247 absolute value was greater than or equal to the absolute value of the observed z-value

248 (Pinheiro & Bates 2000).

249

250 **Results**

251 The average percentage of leaves damaged in this study was 53.6%. The species of

252 the plant had a large effect on the estimated proportional leaf damage, with estimated

253 variance for the species random effect of 2.4 compared with 0.26 for the plot random effect

254 and 0.82 for the observation random effect (equivalent in this model to residual variance).

255 Leaf damage rates ranged from 5% for the non-native highly defended *Euphorbia cyparissias*

256 to close to 98% for the (also non-native) forage legume *Medicago sativa* (Fig. 2). Most of the

257 common, native species such as *Solidago canadensis*, *Asclepias syriaca* and *Symphyotrichum*

258 *spp.* had intermediate to high levels of herbivory (Fig. 2).

259 Sampling date was positively related to estimated proportional leaf damage but not

260 significantly so (z = 1.05, p = 0.334; Table 2).

261 After accounting for species composition, I found a significant positive main effect of

262 species richness (z = 2.26, p = 0.042), and a near-significant negative main effect of

263 phylogenetic diversity (z = -0.19, p = 0.055) on herbivory at the plot-level (Table 2, Fig. 3).

264 There was also a significant negative interaction between phylogenetic diversity and species

265 richness of plants (z = -2.27, p = 0.043; Table 2, Fig. 3), so that the positive effect of species

266 richness on herbivory decreased with increasing phylogenetic diversity. This means that the

267 plots with the highest estimated proportional leaf damage were plots with many species

268 which tended to be closely related. Plots with few species and plots with more distantly

269 related species tended to have lower herbivory (Fig. 3). Plots with the lowest phylogenetic

270 diversity and the highest species richness had about twice as much proportional leaf damage

271   (~80%) as plots with high phylogenetic diversity and low species richness (~40%, Fig 3).

272

273   **Discussion**

274   The results of this study show that phylogenetic diversity is a useful measure for

275   predicting the level of herbivory in plant communities. I have shown that community-level

276   herbivory tends to increase with plant species richness, consistent with some past studies, and

277   in contrast to other past studies (Table 1). On the other hand, I also showed, for the first time,

278   that high phylogenetic diversity of plant communities is associated with overall lowered

279   levels of herbivory. More importantly, there was an interaction between plant species richness

280   and phylogenetic diversity, such that with increasing phylogenetic diversity, the positive

281   effects of species richness on herbivory decrease. This means that the effects of plant species

282   richness on herbivory is dependent on the level of phylogenetic diversity in the plant

283   community (and vice versa).

284

285   *The effects of plant species richness on herbivory*

286   The positive effect of plant species richness on herbivory (at the mean level of

287   phylogenetic diversity) found here is the opposite of early ecological predictions (Elton 1958;

288   Root 1973), but is not surprising given the frequency with which this pattern has been found

289   in other systems (e.g. Mulder & Huss-Danell 2001; Prieur-Richard et al. 2002; Scherber et al.

290   2006; Vehviläinen, Koricheva, & Ruohomäki 2007; Lau et al. 2008; Schuldt et al. 2010; Plath

291   et al. 2011; see Table 1). Theory predicting decreased levels of herbivory in speciose

292   communities was based on the idea that specialist herbivores would be less likely to find and

293   more likely to abandon diverse patches because abundance of their preferred hosts would

294   necessarily be low in such communities (the Resource Concentration Hypothesis : Root

295   1973). However, this theory is dependent on the herbivore species' being monophagous.

296   Thus, in systems where monophages are rare or do not constitute the most damaging class of

297   herbivores, the Resource Concentration Hypothesis is unlikely to apply. Another theory for

298   why herbivore abundance and thus herbivory may be low in speciose plant communities is

299   the Enemies Hypothesis (Elton 1958; Root 1973), which suggests that predators will be more

300   abundant in diverse plant communities, and they will suppress herbivore populations.

301   However, several recent empirical tests of this hypothesis have shown little direct relationship

302   between plant species richness and predator abundance (Scherber *et al.* 2010a; Schuldt *et al.*

303   2011).

304   Theory for potential causes of a positive relationship between species richness and

305 herbivory, on the other hand, is less developed and less frequently cited. Some authors have
306 suggested that this may be the result of nutritional advantages to generalist herbivores who
307 have access to a variety of food resources in diverse patches (Bernays *et al.* 1994; Unsicker
308 *et al.* 2008; Schuldt & Baruffol 2010), which I refer to here as the Dietary Mixing
309 Hypothesis. Other authors have suggested that spillover from preferred to less preferred host
310 species could explain the effect, sometimes referred to as 'associational susceptibility' (White
311 & Whitham 2000).
312   On the other hand, the relationship between plant species richness and herbivory
313 depends on the level of plant phylogenetic diversity you measure it at (the main effect is
314 measured at the mean level of phylogenetic diversity – a natural place to do so). The
315 implication of the significant interaction I found between plant species richness and plant
316 phylogenetic diversity in explaining herbivore damage is that the phylogenetic diversity of
317 the plots alters how species richness affects herbivory. I devote the next section to explaining
318 how this interaction can be potentially explained as a natural outcome of a few simple
319 principles.
320
321 *The effects of plant phylogenetic diversity on herbivory (as mediated through plant species*
322 *richness)*
323   The likelihood of the Resource Concentration Hypothesis, the Dietary Mixing
324 Hypothesis, or associational susceptibility being a factor may be related to the phylogenetic
325 structure of the plant community, because many herbivore species, and especially insect
326 herbivores, have phylogenetic structure in their diet – they feed on few or many species
327 which tend to be closely related (Ehrlich & Raven 1964; Janzen 1980; Ødegaard *et al.* 2005;
328 Weiblen *et al.* 2006; Gossner *et al.* 2009; Futuyma & Agrawal 2009). And so theory which is
329 based on the dichotomy of specialist vs generalist herbivores is likely to be too simplistic to
330 adequately describe real systems. Instead it is more useful to use three categories of herbivore
331 which may inhabit a plant community: 1) True specialists or monophages – which feed on
332 only a single plant species, 2) Phylogenetic specialists or cladophages – which feed on a
333 group of related plant species, and 3) true generalists or polyphages – which feed on a group
334 of plant species which has no pattern with respect to phylogeny at some relevant phylogenetic
335 scale.
336   Though some authors use the term specialist and oligophage in a way consistent with
337 the use of cladophage here – i.e. it is implied or explicitly stated that the author is using those
338 terms to refer to species that feed on more than one closely related species – these terms are

339 also used in other ways. Oligophage literally means a species that feeds on a 'few' hosts

340 (oligo- is latin for 'few'), but does not specify whether these species are poly-, para-, or

341 mono-phyletic. And the term 'specialist' usually needs qualification – e.g. a frugivore can be

342 called a fruit specialist, and a cladophage can be called a phylogenetic specialist. It may then

343 be tempting to conclude that I am introducing the term 'cladophage' because I am tired of

344 typing out the much longer 'phylogenetic specialist' repeatedly. There is value to concision,

345 but I hope the term cladophage will be useful for more than this.

346   The term cladophage can be more precisely defined as a species whose diet consists

347 of other organisms that are more closely related than expected by chance. This means there is

348 some vagueness to the term, as there are multiple ways to decide what is expected by chance

349 (two methods for doing so can be found in Ødegaard et al. 2005, and Weiblen et al. 2006),

350 which depend to some extent on what one is considering the potential diet pool. For example,

351 the phylogenetic scale of the diet pool is important because almost any species can be

352 considered a cladophage at some phylogenetic scale. For example, all insect herbivores are

353 cladophages at the scale of the tree of life, because they only eat plants – a monophyletic

354 clade. Another example is Milkweed Beetles (*Tetraopes* spp.), which only feed on Milkweed

355 plants (Asclepias spp.), and so are cladophages when considering all possible plants. On the

356 other hand, if you are only interested in Milkweed species as a potential diet pool, then

357 Milkweed Beetles may not be considered cladophages because their diet could be random

358 with respect to phylogeny within the Milkweed genera (Farrell and Mitter 1998). And so to

359 properly define these categories, the phylogenetic scale of interest must also be defined.

360 Practically speaking, for the study of herbivory, this will usually be based on the phylogenetic

361 tree containing all the plant species present in the study, which will usually be the most

362 appropriate for understanding local ecological dynamics (Cavender-Bares *et al.* 2009). This

363 definition then potentially includes species whose diets are paraphyletic, as well as

364 monophyletic. It should be noted that other terms contain some such relativity, including

365 monophage. That is, a monophage is defined as a species that only eats one other organism,

366 but it can be measured as what a species is observed to eat in its natural habitat, or as what a

367 species potentially could eat, if given the opportunity. A monophage in a particular habitat

368 may not be a monophage in another where some new host species becomes available. This

369 concept of 'effective' specialization is important to understanding why phylogenetic diversity

370 might affect the relationship between host species richness and herbivory.

371   Using this framework we can begin to make hypotheses about the effects that

372 phylogenetic diversity might have on herbivory in plant communities. It is clear that neither

373 monophages nor polyphages should be affected by phylogenetic diversity of plants, at least

374 directly – though nutritional effects are possible in generalists. On the other hand,

375 cladophages are likely to respond to phylogenetic diversity of plants due to direct interactions

376 with their host-plants (Dinnage et al. 2012). In a plant community with low phylogenetic

377 diversity, if one host capable of supporting a particular cladophage is present, there is likely

378 to be other suitable hosts as well (assuming the presence of at least moderate species

379 richness). On the other hand, in plant communities with high phylogenetic diversity, if any

380 hosts are suitable for a particular cladophage, it is likely to be the only one. This means that

381 cladophages present in low phylogenetic diversity plant communities will be 'effective

382 polyphages'; cladophages present in high phylogenetic diversity plant communities will be

383 'effective monophages'. Therefore, in plant communities with low phylogenetic diversity,

384 cladophages are more likely to be able to take advantage of dietary mixing effects (as per the

385 Dietary Mixing Hypothesis), and so species richness should have a positive effect. This is

386 consistent with how phylogenetic diversity changed the effect of plant species richness on

387 herbivory observed in this study – that is, the positive effect of species richness increased at

388 low phylogenetic diversity, and decreased at high phylogenetic diversity (Fig. 3).

389   In plant communities with high phylogenetic diversity, cladophages will usually only

390 be able to feed on one or a very few species, and so they may respond according to the

391 Resource Concentration Hypothesis, that is, increasing the number of species in the plant

392 community will make it more difficult for them to find their preferred host. Though in this

393 study, the effect of species richness never became negative even at the highest level of

394 phylogenetic diversity, it did become very nearly flat (Fig. 3). It is possible that the

395 relationship would have become negative if there had been plots in this study with even

396 higher phylogenetic diversity than observed.

397   There are several reasons why the relationship between plant species richness and

398 herbivory may not become completely negative at the highest phylogenetic diversity of

399 plants. For one, the effects of cladophages will be overlaid on the effects from monophages

400 and polyphages. If the polyphage effect is more important in the system, then positive effects

401 of plant species richness will likely predominate. Another possibility is that low species

402 richness can sometimes have a negative effect on monophages, instead of the expected

403 positive effect according to the Resource Concentration Hypothesis. These effects have been

404 termed 'resource dilution effects' (Otway, Hector, & Lawton 2005), and the commonness of

405 their occurrence has yet to be established.

406   Even though the effect of phylogenetic diversity on herbivory depended on plant

407   species richness, the overall main effect – measured at the mean level of plant species

408   richness – was negative, suggesting that in this system, there is an average decline in

409   herbivory with phylogenetic diversity. Though no previous study has looked at the role of

410   phylogenetic diversity *per se* on rates of herbivory in plant communities, my results are

411   consistent with the results of Jactel & Brockerhoff (2007), who found in a meta-analysis that

412   reductions in herbivory for focal trees grown in mixed stands instead of monoculture stands

413   were stronger when the associated tree species in the mixed stand was taxonomically

414   unrelated to the focal species.

415

416   *The role of cladophages in ecological systems*

417   The relative abundance of cladophages in this system is unknown, but it is likely that

418   they occur regularly in most systems. It has been noted that the tendency for herbivores to

419   feed on several closely related species is widespread (Ehrlich & Raven 1964; Janzen 1980;

420   Futuyma & Agrawal 2009). If so, it is predicted that insect herbivore assemblages should be

421   more similar in closely related plant hosts than in more distantly related ones. This pattern

422   has been found in several recent studies in different systems (Ødegaard *et al.* 2005; Weiblen

423   *et al.* 2006; Gossner *et al.* 2009). For example, in a tropical system, Weiblen *et al.* (2006)

424   found that approximately half of the herbivore species they studied could be categorized as

425   phylogenetic specialists.

426   The widespread existence of cladophages is also an assumption underlying the

427   hypothesis that invasive species which are more distantly related to native species should

428   experience higher levels of enemy release and thus lower levels of herbivory (Mitchell *et al.*

429   2006). This pattern, too, has been found in several recent studies (Dawson, Burslem, &

430   Hulme 2009; Hill & Kotanen 2009; Ness, Rollinson, & Whitney 2011). Native species have

431   also been shown to experience lower herbivory when growing with neighbours which are

432   distantly related (Yguel *et al.* 2011; Ness *et al.* 2011), further suggesting not only that

433   cladophages are common, but that they exert important influence in ecological systems.

434

435   *Alternative explanations*

436   There are several alternative explanations for why phylogenetic diversity might

437   indirectly affect herbivory. It has been suggested that phylogenetic diversity is a good proxy

438   for unmeasured trait or functional diversity of a community (e.g. Cadotte et al. 2008;

439   Cavender-Bares et al. 2009). It is possible that functional diversity may be responsible for

440   reduced herbivory. It is not clear why functional diversity would decrease herbivory directly,

441   but it is possible that increased functional diversity could promote predator recruitment and

442   abundance, which in turn could suppress herbivores. Functional diversity could increase the

443   architectural complexity of a plot, allowing more hunting niches, nesting sites, and places to

444   hide and stalk for predators (Andow & Prokrym 1990; Coll & Botrell 1996; Beals 2006;

445   Woodcock *et al.* 2007). For example, Dinnage et al. (2012) found that in an experimental

446   prairie system, predator abundance increased strongly with phylogenetic diversity. However,

447   in the old field system at my study site, there was little variation in structural forms. Most

448   species grew with tall stalks, and leaves parallel to the ground along their entire height. There

449   were a few understory species (rosettes), a few vines, and a few tree or shrub saplings. Most

450   plots had all of these, regardless of phylogenetic diversity (Table S1, personal observation).

451   These growth forms occurred across the phylogenetic tree without any obvious patterns.

452   However, I cannot rule out this explanation without further information on the abundance of

453   predators. The effect may also have been the result of a combination of factors, that is, both

454   increased predator abundance and reduced diet breadth are jointly responsible for the

455   decrease in herbivory.

456   It is possible that a correlation between phylogenetic and functional diversity

457   contributes to the patterns I observed in addition to the effects of cladophagy, but it does not

458   offer a good explanation for the interaction between phylogenetic diversity and species

459   richness, or the effect of species richness itself. This is because functional diversity is also

460   expected to – and usually observed to – increase with species richness, and in fact this is

461   often the explanation offered for why species richness affects various ecosystem functions

462   (Tilman 1997; Loreau *et al.* 2001; Hooper *et al.* 2005; Cardinale *et al.* 2006; Balvanera *et al.*

463   2006; Duffy *et al.* 2007; Cadotte *et al.* 2009; Fornara & Tilman 2009; Cardinale 2011;

464   Connolly *et al.* 2011). Given this, we should expect to see a synergy between phylogenetic

465   diversity and species richness, rather than a negative interaction.

466   Though the observational nature of this study gives it the advantage of realism, it also

467   means I cannot completely rule out all confounding factors that may explain my results. If,

468   for example, there were abiotic conditions which influenced both species richness and

469   phylogenetic diversity, and also affected herbivory, and which varied sufficiently across my

470   sites, this could spuriously generate the observed correlations (Proches et al. 2009). Though

471   all the plots in this study came from a small geographic area and from a single habitat type,

472   and thus likely do not vary much in environmental conditions, it is possible that some soil

473   characteristics may have varied between the plots. Though environmental correlates of

474   species richness have attracted much interest in the past, especially at large spatial scales,

475 little is known about what environmental factors might influence phylogenetic diversity.

476 Since it is often supposed that phylogenetically closely related species will compete more

477 strongly, it is possible that plots with conditions that suppress competition amongst plants are

478 the only ones where many species which are closely related can coexist. If such conditions

479 also promoted high herbivory, then this could lead to high herbivory in plant communities

480 with high species richness and low phylogenetic diversity, as observed. To fully understand

481 the role of phylogenetic diversity in ecosystem function will require conducting large-scale

482 experiments where phylogenetic diversity is explicitly manipulated, but observational studies

483 in natural settings such as this will remain invaluable.

484

485 *Limitations of this study: Measuring the impact of herbivory*

486   This study shows that many plants may receive lower herbivore damage in

487 phylogenetically diverse communities. This result is similar to those of Yguel *et al.* (2011)

488 who found that oak trees that grew amongst distantly related trees experienced lower

489 herbivory. Yguel *et al.* (2011) suggested that this may produce a selective benefit that could

490 promote the evolution of a strategy to grow amongst distant relatives. This is an intriguing

491 possibility, but studies which only measure the magnitude of damage on plants cannot draw

492 this conclusion, unless they also measure the impact of damage on the plants. In order to

493 understand how selection might affect a plants' preference for its phylogenetic

494 neighbourhood, we need to know how the fitness of the plants are affected.

495   Damage is generally thought of as a negative impact on plant fitness, but many plants

496 are able to tolerate large amounts of damage without sustaining large reductions in fitness

497 (Rosenthal & Kotanen 1994; Strauss & Agrawal 1999). To understand fitness impacts of

498 herbivory generally requires measuring plant performance in the presence and absence of

499 herbivory. In Table 1, I show that although many studies that looked at the magnitude of

500 herbivory found that plant species richness increased herbivory, all but two studies that

501 looked at the impact of herbivory found a negative association with plant species richness,

502 such that speciose communities had a smaller difference in biomass between herbivore

503 exclusion and control treatments. This suggests that plant diversity may provide benefits in

504 terms of a plant's ability to tolerate herbivory, which more than makes up for any increases in

505 the actual amount of herbivore damage.

506   I therefore cannot conclude that any reduction in herbivory due to high phylogenetic

507 diversity *necessarily* results in an advantage to plants growing with their distant relatives.

508 However, the only way this would not be the case is if plants growing in low phylogenetic

509 diversity communities were more tolerant of damage than plants growing in high

510 phylogenetic diversity communities, and this increase in tolerance fully compensated for the

511 increase in herbivore damage. This seems unlikely, but cannot be ruled out without herbivore

512 exclusion studies. It is possible, for example, that plants growing with distant relatives will

513 tend to be in more marginal habitat, since abiotic niche requirements also may be similar for

514 close relatives (Cavender-Bares *et al.* 2009). Plants in marginal habitat may be impacted by

515 herbivory more.

516

517 *Implications for other studies*

518   As I show in Table 1, the results of previous studies are inconsistent about the

519 relationship observed between herbivory and species richness. The interaction I observed

520 between phylogenetic diversity and species richness in this study may offer an explanation.

521 That is, the degree and even direction of the relationship between species richness and

522 herbivory may depend on the difference in phylogenetic diversities of the communities that

523 are compared. Though I observed such a relationship at a local scale, between individual

524 plots, it may also apply on a larger scale. For example, it is possible that I may have observed

525 an overall positive main effect of species richness in my study because there was generally a

526 low amount of phylogenetic diversity in this system compared with other systems. Old fields

527 tend to be dominated by species in the family Asteraceae, and the one I studied is no

528 exception. Other systems where the question has been studied may draw from a larger pool of

529 evolutionary history, where negative effects may perhaps be more likely.

530   Of course, the relative abundance and importance of monophages, polyphages, and

531 cladophages present and active in the plant communities may also alter the observed effect of

532 plant diversity. For example, simplified ecosystems such as agricultural systems – where we

533 often see negative diversity-herbivory relationships (Andow 1991) – may be dominated by

534 monophages, because monocultures on very large scales may discourage polyphages (or even

535 many cladophages). Whereas polyphages need not be less common compared with

536 monophages in monocultures that are imbedded in a more diverse landscape (as is the case

537 for most biodiversity experiments), as long as the scale of the plots does not exceed the

538 dispersal capability of the polyphages. In natural ecosystems, some systems may be more

539 dominated by extinction-recolonization dynamics of both plants and herbivores, whereas

540 others may be dominated by relatively stable populations of low-dispersal plant and

541 herbivores, which could also have major effects of Resource Concentration and Dietary

542 Mixing. All else being equal, I suggest that the phylogenetic or phenotypic diversity is likely

543 to play a strong role, in addition to the other factors.

544

545 *Conclusion*

546   Here I have shown that incorporating measures of phylogenetic diversity can improve

547 our understanding of the role of plant diversity in promoting or suppressing herbivore

548 damage. Phylogenetic diversity was negatively correlated with herbivory in an old field

549 system, and determined the degree to which species richness influenced herbivory as well. If

550 we consider a reduction in herbivore damage as a positive outcome at the community scale,

551 as is often the case in agricultural ecosystems, then we may wish to prioritize the

552 conservation and restoration of phylogenetic diversity, perhaps even at the expense of some

553 species richness.

554

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559

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Table 1(on next page)

Literature review of previous studies on the role of plant diversity in promoting or supressing herbivory

Type refers to whether the species richness was manipulated (Experimental), natural species richness variation was taken advantage of (Observational), or the conclusion was based on estimates from previous literature (Meta-analysis). No study from the meta-analyses were repeated in this table. Consumer effect refers to whether the study estimated a measure of the amount of interaction between plants and consumers (Magnitude) – usually a damage measurement, or estimated the effect that interaction had on the plants' fitness (Impact) – usually by measuring biomass in the presence or absence of herbivory. A positive relationship means that the study found that the magnitude or impact of herbivory increased with increasing plant diversity, a negative relationship means the study found that herbivory decreased with plant diversity. None means the study found no relationship between herbivory and plant diversity

Study	Type	Species Richness Range	Measured	Measured On effect	Consumer	Relationship
Lau et al. 2008	Experimental	1 vs. 16	Leaf damage from generalists	1 Legume sp	Magnitude	Positive
Mulder & Huss-Danell 2001	Experimental	1, 2, 4, 8, 12	Leaf damage	Community	Magnitude	Positive
Plath et al. 2011	Experimental	1 vs. 3	Leaf damage	1 Rosea tree	Magnitude	Positive
Prieur-Richard et al. 2002	Experimental	3, 6, 18	Leaf damage	2 Conyza spp.	Magnitude	Positive
Scherber et al. 2006	Experimental	1, 2, 4, 8, 16, & 60	Leaf damage	All species + 3 phytometer spp	Magnitude	Positive
Schuldt et al. 2010	Observational	25 – 68	Leaf damage	10 tree spp	Magnitude	Positive
Vehviläinen, Koricheva & Ruohomäki 2007	Meta-analysis	1 vs. Several	Leaf damage	2 tree spp (Oak & Alder)	Magnitude	Positive
Wang et al. 2010	Observational	1,2,4,6,8,11	# plants grazed by sheep	Community	Magnitude	Positive
Hanley 2004 relationship	Experimental	3, 6, 12	Leaf damage by Mollusks	All spp	Magnitude	No
Sobek et al. relationship 2009	Observational	Natural range across German deciduous forest	Leaf damage by insects	2 Maple spp	Magnitude	No
Yguel et al. relationship 2011	Observational	Natural range across managed French forest	Leaf damage	1 Oak sp.	Magnitude	No
Jactel & Brock-erhoff 2007	Meta-analysis	1 vs. Several	Leaf damage	Many individual spp.	Magnitude	Negative
Lau et al. 2008	Experimental	1 vs. 16	Leaf damage from specialists	1 Legume sp	Magnitude	Negative
Massey et al. 2006	Experimental	1 vs. 5	Leaf damage	1 Shorea sp	Magnitude	Negative
McNaughton 1985	Observational	Natural range across Serengeti	% Biomass consumed	Community	Magnitude	Negative
Petermann et al. 2010	Experimental	1, 2, 3, 4, 6, 9	Infestation by aphids	Community	Magnitude	Negative
Sobek et al. 2009	Observational	Natural range across German deciduous forest	Leaf damage by insects	1 Beech sp	Magnitude	Negative

Unsicker et al. 2006	Observational	18 – 45	Leaf damage	Many individual spp.	Magnitude	Negative
Vehviläinen, Koricheva & Ruohomäki 2007	Meta-analysis	1 vs. Several	Leaf damage by insects	1 Birch sp	Magnitude	Negative
Wilsey & Polley 2002	Experimental	1 – 4 (manipulated Evenness)	Infestation by spittlebugs	Solidago canadensis	Magnitude	Negative
Mulder & Huss-Danell 2001	Experimental	1, 2, 4, 8, 12	Reduction of biomass in insecticide plots	Community	Impact	Positive
Scherber et al. relationship 2010	Experimental	1, 2, 4, 8, 16, 60	% reduction of biomass in insect exclusions	Community	Impact	No
Hillebrand & Cardinale 2004	Meta-analysis	1 - 60	Absolute and % reduction of bio-mass in grazer exclusion	Community of phytoplankton	Impact	Negative
Lanta 2007	Experimental	1, 2, 4, 6	Reduction of biomass in Mol-lusk exclusions	Community	Impact	Negative
Narwani & Mazumder 2010	Experimental	1 vs. 4	Biomass consumed	Community of phytoplankton	Impact	Negative
Pfisterer, Diemer & Schmid 2003	Experimental	1, 2, 4, 8, 32	% reduction of biomass in insect exclusion	Community	Impact	Negative
Stein et al. 2010	Observational	15 – 37	% reduction of biomass in insect exclusions	Community	Impact	Negative

Figure 1

Phylogenetic tree with branch lengths representing all species in this study

Species highlighted in grey are species for which herbivore damage measurements were taken. Branch lengths represent divergence times. Methods for generating the tree can be found in Dinnage (2009).
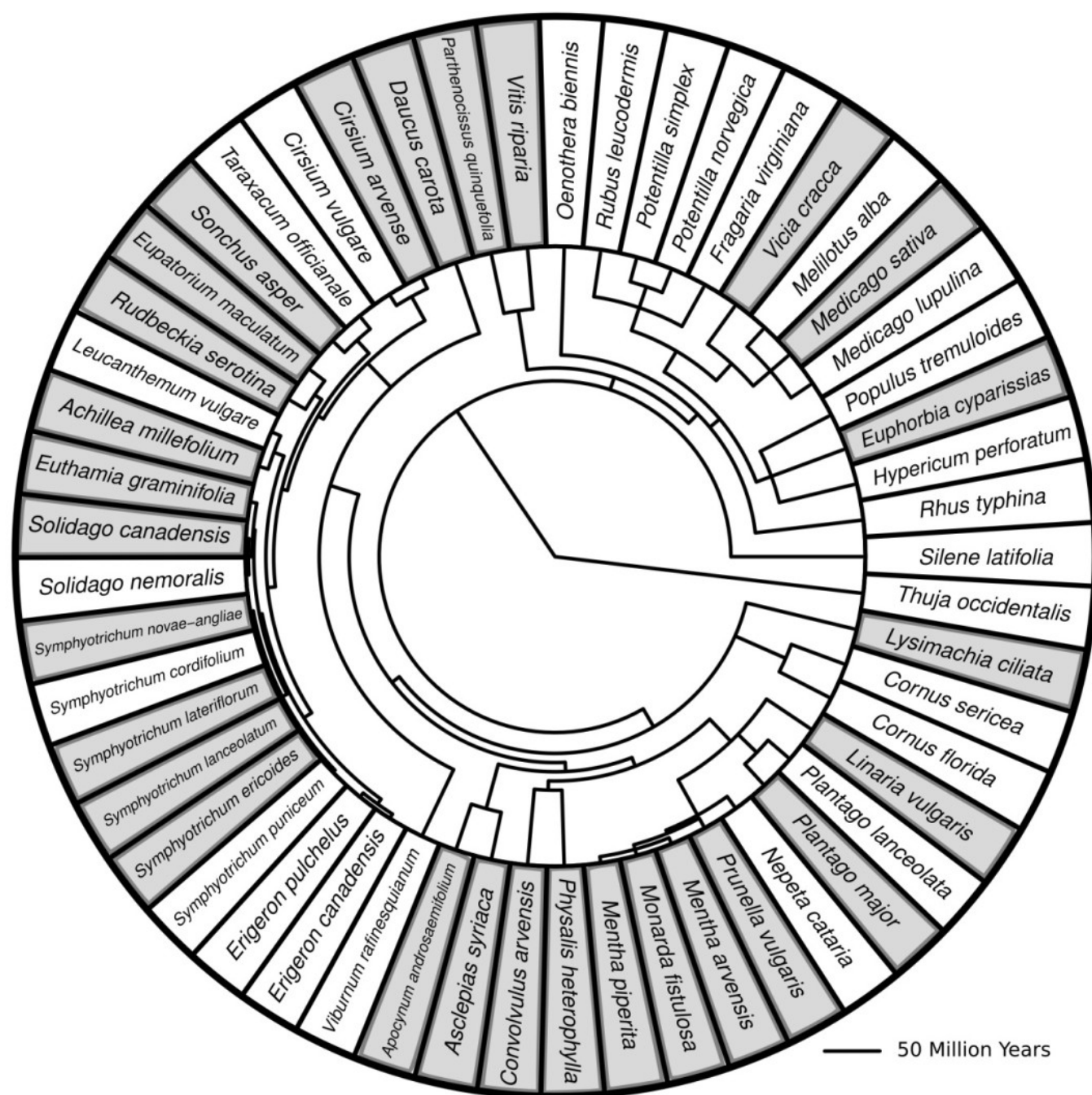
Figure 2

Species-level herbivory of the 27 species for which herbivore damage measurements were taken

On the left is the phylogenetic relationships of the species with branch length representing time since divergence. On the right is a barchart whose bars represent the best linear unbiased predictors (BLUPs) or conditional modes of the estimated proportional leaf damage for each species. Error bars are based on the conditional variance-covariance matrix generated by the model fitting procedure (lmer function in the lme4 package for R) and are conditional mode +/- 1 conditional standard deviation.
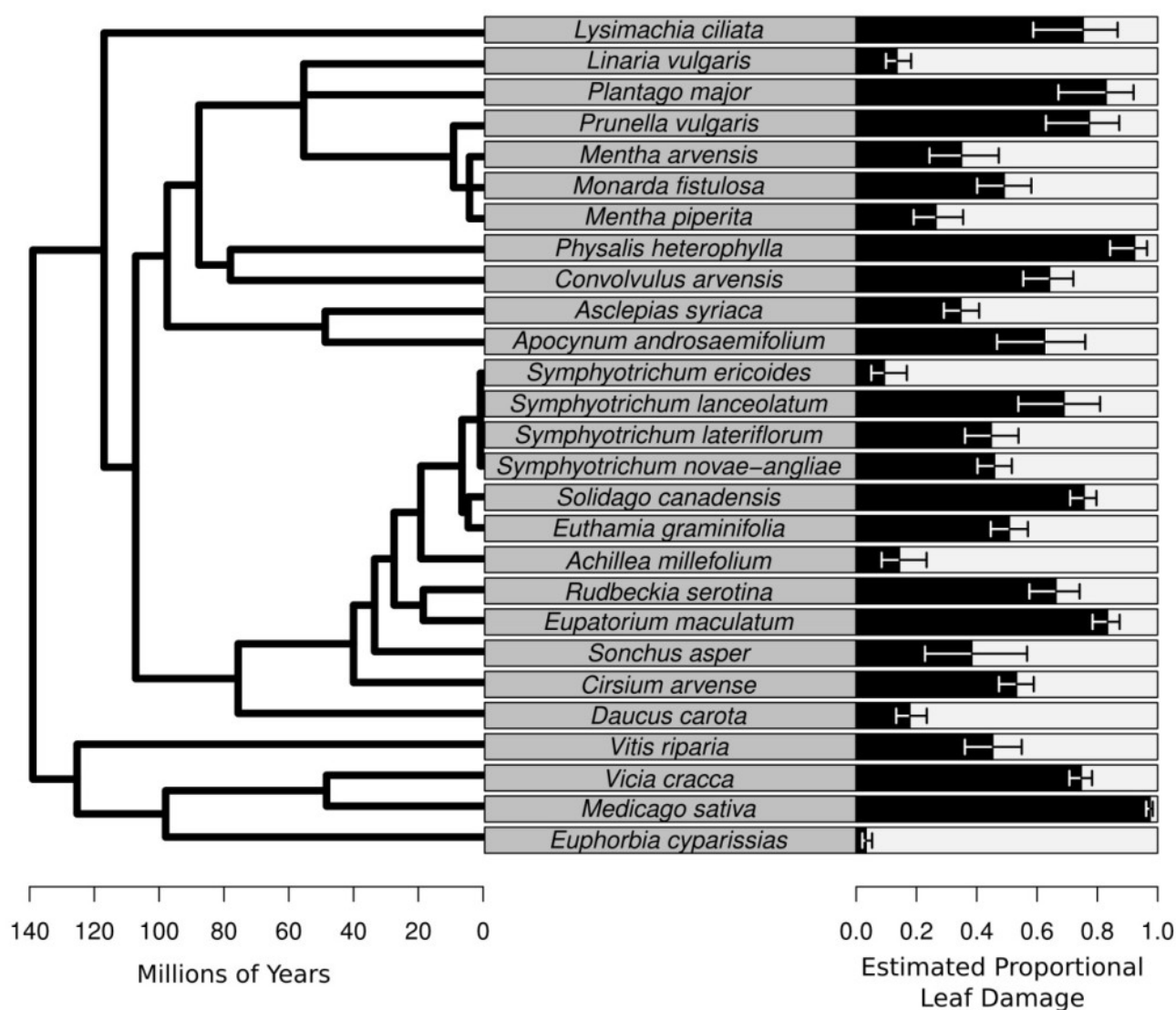
Table 2 (on next page)

Statistics for the fixed effects

Statistics for the fixed effects in a generalized linear mixed model (GLMM) with binomial family and logit link. $\Pr(|z|_{obs} < |z|_{sim})$ is the p-value generated from a parametric bootstrap on the z values. * z value is significant at the alpha = 0.05 level.

Parameter	Name of Factor	Estimate	z value	$\Pr(|z|_{obs}<|z|_{sim})$
α	Intercept	0.15		
β_{date}	Sampling Date	0.10	1.05	0.334
β_{sr}	Plant Species Richness	0.23	2.26	0.042*
β_{pd}	Plant Phylogenetic Diversity (PSE)	-0.19	-2.10	0.055
β_{sr*pd}	Plant Diversity Interaction	-0.28	-2.27	0.043*

Figure 3

Two figures showing the relationship between estimated proportional leaf damage and plot-level plant species richness and phylogenetic diversity.

a) Points represent best linear unbiased predictors (BLUPs) or conditional modes of plots. The size of the points is proportional to the species richness of the plot so that large points are speciose communities. Error bars are based on the conditional variance-covariance matrix generated by the model fitting procedure (lmer function in the lme4 package for R) and are conditional mode +/- 1 conditional standard deviation. Fitted lines are back-transformed predicted values from the full generalized linear mixed model, for four different pre-set values of species richness (3,6,12,&17) representing the full range of species richnesses in this study. b) A heatmap which shows the back-transformed fitted surface of the full generalized linear mixed model. Points are the plot BLUPs, their colour represents their value as per the legend. Points that are darker than the surrounding colour fall below the predicted surface; points which are lighter fall above it.