Species richness and phylogenetic diversity have opposing effects 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

33

34   The insect herbivore flies, crawls, hovers, and feeds in a matrix of stems, roots,

35   flowers and leaves. Thousands do this in a typical community of plants in what – to us – is an

36   impenetrably complex tangle of traits, each the product of millions of years of evolution.

37   How then are we to understand the aggregate patterns that emerge from such a community?

38   Indeed, community ecologists have long struggled to understand how the identity and traits of

39   individual plant species add together and interact to determine herbivore communities and the

40   damage they cause.

41   Though much work on insect herbivory has focused on interactions between single

42   pairs of insect and plant species, it is also important to understand the phenomenon at the

43   level of whole plant communities. After all, many of the consequences of major ecosystem

44   changes will be manifest at the level of the community, and one-to-one interactions may not

45   always be additive (Agrawal, Lau, & Hamback 2006; Agrawal *et al.* 2007).

46   One way of understanding herbivory at the community level is to look at the effects of

47   plant species richness. Plant species richness is one of the simplest way to summarize

48   information about many species at the community level, and studies of its role in herbivory

49   link up nicely with the body of literature on the relationship between diversity and ecosystem

50   functioning (Siemann *et al.* 1998; Haddad *et al.* 2001; Loreau *et al.* 2001; Hooper *et al.* 2005;

51   Cardinale *et al.* 2006; Balvanera *et al.* 2006; Cardinale *et al.* 2007; Scherber *et al.* 2010a).

52   Insect herbivore damage is a useful reflection of the activities of insect herbivores in plant

53   communities, as well as a phenomenon of interest in and of itself, with implications for the

54   health of a plant community.

55   There are some clear theoretical predictions about the effects of plant species richness

56   on herbivory, which derive from a simple understanding of direct trophic interactions

57   between plants and insects. Root (1973) suggested that increased plant species richness

58   should lead to a decrease in specialist herbivores, and thus to a decrease in herbivory. The

59   Resource Concentration Hypothesis states that if the number of plant species in a patch is

60   higher, the density of each plant species must be lower, and so specialist herbivores of those

61   species will be less likely to find such a patch, stay in such a patch, and do damage in such a

62   patch. On the other hand, the presence of a wide variety of plant species provides a wide

63   variety of nutritional resources for generalist herbivores, which may prefer to eat in diverse

64   patches, and may thrive more in them too (Unsicker *et al.* 2008; Schuldt & Baruffol 2010). I

65   will refer to this idea as the Dietary Mixing Hypothesis (after Bernays et al. 1994).

66   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 occurence 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.

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

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

113

114 Materials and methods

115 *Data collection*

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

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

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

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

120 research there.

121

122 *Species survey*

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

140

141 *Herbivory survey*

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

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

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

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

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

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

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

149

150 *Phylogeny and diversity indices*

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

167 2011). PSE ranges between 0 and 1, where high values are associated with high phylogenetic

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

169 clustering – small average phylogenetic distances among species in the community.

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

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

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

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

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

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

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

177 quantities with no simple interpretation biologically. I did calculate evenness for the plots and

178 it was not correlated with phylogenetic diversity, and so the phylogenetic diversity measure,

179 though abundance-weighted, was not confounded with species evenness. In addition,

180 evenness was not a significant predictor of herbivory when included as a factor in the model

181 described below, and so I did not use it.

182

183 *Statistical analysis*

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

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

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

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

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

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

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

191

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

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

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

196

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

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

199 $PD_{plot[i]}$ and $SR_{plot[i]}$ are the phylogenetic diversity and the species richness, respectively, for

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

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

202 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

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

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

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

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

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

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

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

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

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

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

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

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

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

216 variables.

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

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

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

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

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

222 1000 such simulations, and a p value determined as the percent of simulated z values whose

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

224 (Pinheiro & Bates 2000).

225

226 **Results**

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

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

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

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

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

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

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

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

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

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

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

238   species richness (z = 2.26, p = 0.042), and a marginally significant negative main effect of

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

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

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

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

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

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

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

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

247   (~80%) as plots with high phylogenetic diversity and low species richness (~40%, Fig 3).

248

249   Discussion

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

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

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

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

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

255   levels of herbivory. Even more importantly, there was an interaction between plant species

256   richness and phylogenetic diversity, such that with increasing phylogenetic diversity, the

257   positive effects of species richness on herbivory decrease.

258

259   *The effects of plant species richness on herbivory*

260   The positive effect of plant species richness on herbivory found here is the opposite of

261   early ecological predictions (Elton 1958; Root 1973), but is not surprising given the

262   frequency with which this pattern has been found in other systems (e.g. Mulder &

263   Huss-Danell 2001; Prieur-Richard et al. 2002; Scherber et al. 2006; Vehviläinen, Koricheva,

264   & Ruohomäki 2007; Lau et al. 2008; Schuldt et al. 2010; Plath et al. 2011; see Table 1).

265   Theory predicting decreased levels of herbivory in speciose communities was based on the

266   idea that specialist herbivores would be less likely to find and more likely to abandon diverse

267   patches because abundance of their preferred hosts would necessarily be low in such

268   communities (the Resource Concentration Hypothesis : Root 1973). However, this theory is

269   dependent on the herbivore species' being monophagous. Thus, in systems where

270   monophages are rare or do not constitute the most damaging class of herbivores, the

271 Resource Concentration Hypothesis is unlikely to apply. Another theory for why herbivore
272 abundance and thus herbivory may be low in speciose plant communities is the Enemies
273 Hypothesis (Elton 1958; Root 1973), which suggests that predators will be more abundant in
274 diverse plant communities, and they will suppress herbivore populations. However, several
275 recent empirical tests of this hypothesis have shown little direct relationship between plant
276 species richness and predator abundance (Scherber *et al.* 2010a; Schuldt *et al.* 2011).

277 Theory for potential causes of a positive relationship between species richness and
278 herbivory, on the other hand, is less developed and less frequently cited. Some authors have
279 suggested that this may be the result of nutritional advantages to generalist herbivores who
280 have access to a variety of food resources in diverse patches (Bernays *et al.* 1994; Unsicker
281 *et al.* 2008; Schuldt & Baruffol 2010), which I refer to here as the Dietary Mixing
282 Hypothesis. Other authors have suggested that spillover from preferred to less preferred host
283 species could explain the effect, sometimes referred to as 'associational susceptibility' (White
284 & Whitham 2000).

285

286 *The effects of plant phylogenetic diversity on herbivory*

287 The likelihood of the Resource Concentration Hypothesis, the Dietary Mixing
288 Hypothesis, or associational susceptibility being a factor may be related to the phylogenetic
289 structure of the plant community, because many herbivore species, and especially insect
290 herbivores, have phylogenetic structure in their diet – they feed on few or many species
291 which tend to be closely related (Ehrlich & Raven 1964; Janzen 1980; Ødegaard *et al.* 2005;
292 Weiblen *et al.* 2006; Gossner *et al.* 2009; Futuyma & Agrawal 2009). And so theory which is
293 based on the dichotomy of specialist vs generalist herbivores is likely to be too simplistic to
294 adequately describe real systems. Instead it is more useful to use three categories of herbivore
295 which may inhabit a plant community: 1) True specialists or monophages – which feed on
296 only a single plant species, 2) Phylogenetic specialists or cladophages – which feed on a
297 group of related plant species, and 3) true generalists or polyphages – which feed on a group
298 of plant species which has no pattern with respect to phylogeny at some relevant phylogenetic
299 scale. Phylogenetic scale is important because almost any species can be considered a
300 cladophage at some phylogenetic scale. For example, all insect herbivores are cladophages at
301 the scale of the tree of life, because they only eat plants – a monophyletic clade. And so to
302 properly define these categories, the phylogenetic scale of interest must also be defined.
303 Practically speaking, for the study of herbivory, this will usually be based on the phylogenetic
304 tree containing all the plant species present in the study, which will usually be the most

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

306   Using this framework we can begin to make hypotheses about the effects that
307 phylogenetic diversity might have on herbivory in plant communities. It is clear that neither
308 monophages nor polyphages should be affected by phylogenetic diversity of plants, at least
309 directly – though nutritional effects are possible in generalists. On the other hand,
310 cladophages are likely to respond to phylogenetic diversity of plants due to direct interactions
311 with their host-plants (Dinnage et al. 2012). In a plant community with low phylogenetic
312 diversity, if one host capable of supporting a particular cladophage is present, there is likely
313 to be other suitable hosts as well (assuming the presence of at least moderate species
314 richness). On the other hand, in plant communities with high phylogenetic diversity, if any
315 hosts are suitable for a particular cladophage, it is likely to be the only one. This means that
316 cladophages present in low phylogenetic diversity plant communities will be 'effective
317 polyphages'; cladophages present in high phylogenetic diversity plant communities will be
318 'effective monophages'. Therefore, in plant communities with low phylogenetic diversity,
319 cladophages are more likely to be able to take advantage of dietary mixing effects (as per the
320 Dietary Mixing Hypothesis), and so species richness should have a positive effect. This is
321 consistent with the negative effect of phylogenetic diversity on herbivory observed in this
322 study, and also may explain why the positive effect of species richness increased at low
323 phylogenetic diversity.

324   In plant communities with high phylogenetic diversity, cladophages will usually only
325 be able to feed on one or a very few species, and so they may respond according to the
326 Resource Concentration Hypothesis, that is, increasing the number of species in the plant
327 community will make it more difficult for them to find their preferred host. Though in this
328 study, the effect of species richness never became negative even at the highest level of
329 phylogenetic diversity, it did become very nearly flat (Fig. 3). It is possible that the
330 relationship would have become negative if there had been plots in this study with even
331 higher phylogenetic diversity than observed.

332   There are several reasons why the relationship between plant species richness and
333 herbivory may not become completely negative at the highest phylogenetic diversity of
334 plants. For one, the effects of cladophages will be overlaid on the effects from monophages
335 and polyphages. If the polyphage effect is more important in the system, then positive effects
336 of plant species richness will likely predominate. Another possibility is that low species
337 richness can sometimes have a negative effect on monophages, instead of the expected
338 positive effect according to the Resource Concentration Hypothesis. These effects have been

339   termed 'resource dilution effects' (Otway, Hector, & Lawton 2005), and the commonness of
340   their occurrence has yet to be established.
341   Though no study to date has studied the role of phylogenetic diversity *per se* on rates
342   of herbivory in plant communities, my results are consistent with the results of Jactel &
343   Brockerhoff (2007), who found in a meta-analysis that reductions in herbivory for focal trees
344   grown in mixed stands instead of monoculture stands were stronger when the associated tree
345   species in the mixed stand was taxonomically unrelated to the focal species.
346
347   *The role of cladophages in ecological systems*
348   The relative abundance of cladophages in this system is unknown, but it is likely that
349   they occur regularly in most systems. It has been noted that the tendency for herbivores to
350   feed on several closely related species is widespread (Ehrlich & Raven 1964; Janzen 1980;
351   Futuyma & Agrawal 2009). If so, it is predicted that insect herbivore assemblages should be
352   more similar in closely related plant hosts than in more distantly related ones. This pattern
353   has been found in several recent studies in different systems (Ødegaard *et al.* 2005; Weiblen
354   *et al.* 2006; Gossner *et al.* 2009). For example, in a tropical system, Weiblen *et al.* (2006)
355   found that approximately half of the herbivore species they studied could be categorized as
356   phylogenetic specialists.
357   The widespread existence of cladophages is also an assumption underlying the
358   hypothesis that invasive species which are more distantly related to native species should
359   experience higher levels of enemy release and thus lower levels of herbivory (Mitchell *et al.*
360   2006). This pattern, too, has been found in several recent studies (Dawson, Burslem, &
361   Hulme 2009; Hill & Kotanen 2009; Ness, Rollinson, & Whitney 2011). Native species have
362   also been shown to experience lower herbivory when growing with neighbours which are
363   distantly related (Yguel *et al.* 2011; Ness *et al.* 2011), further suggesting not only that
364   cladophages are common, but that they exert important influence in ecological systems.
365
366   *Alternative explanations*
367   There are several alternative explanations for why phylogenetic diversity might
368   indirectly affect herbivory. It has been suggested that phylogenetic diversity is a good proxy
369   for unmeasured trait or functional diversity of a community (e.g. Cadotte et al. 2008;
370   Cavender-Bares et al. 2009). It is possible that functional diversity may be responsible for
371   reduced herbivory. It is not clear why functional diversity would decrease herbivory directly,
372   but it is possible that increased functional diversity could promote predator recruitment and

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

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

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

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

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

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

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

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

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

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

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

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

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

386   decrease in herbivory.

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

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

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

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

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

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

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

394   2006; Duffy *et al.* 2007; Cadotte *et al.* 2009; Fornara & Tilman 2009; Cardinale 2011;

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

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

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

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

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

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

401   sites, this could spuriously generate the observed correlations. Though all the plots in this

402   study came from a small geographic area and from a single habitat type, and thus likely do

403   not vary much in environmental conditions, it is possible that some soil characteristics may

404   have varied between the plots. Though environmental correlates of species richness have

405   attracted much interest in the past, especially at large spatial scales, little is known about what

406   environmental factors might influence phylogenetic diversity. Since it is often supposed that

407   phylogenetically closely related species will compete more strongly, it is possible that plots

408   with conditions that suppress competition amongst plants are the only ones where many

409   species which are closely related can coexist. If such conditions also promoted high

410   herbivory, then this could lead to high herbivory in plant communities with high species

411   richness and low phylogenetic diversity, as observed. To fully understand the role of

412   phylogenetic diversity in ecosystem function will require conducting large-scale experiments

413   where phylogenetic diversity is explicitly manipulated, but observational studies in natural

414   settings such as this will remain invaluable.

415

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

436   the actual amount of herbivore damage.

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

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

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

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

phylogenetic diversity communities, and this increase in tolerance fully compensated for the increase in herbivore damage. This seems unlikely, but cannot be ruled out without herbivore exclusion studies. It is possible, for example, that plants growing with distant relatives will tend to be in more marginal habitat, since abiotic niche requirements also may be similar for close relatives (Cavender-Bares *et al.* 2009). Plants in marginal habitat may be impacted by herbivory more.

Implications for other studies

As I show in Table 1, the results of previous studies are inconsistent about the relationship observed between herbivory and species richness. The interaction I observed between phylogenetic diversity and species richness in this study may offer an explanation. That is, the degree and even direction of the relationship between species richness and herbivory may depend on the difference in phylogenetic diversities of the communities that are compared. Though I observed such a relationship at a local scale, between individual plots, it may also apply on a larger scale. For example, it is possible that I may have observed an overall positive main effect of species richness in my study because there was generally a low amount of phylogenetic diversity in this system compared with other systems. Old fields tend to be dominated by species in the family Asteraceae, and the one I studied is no exception. Other systems where the question has been studied may draw from a larger pool of evolutionary history, where negative effects may perhaps be more likely.

Of course, the relative abundance and importance of monophages, polyphages, and cladophages present and active in the plant communities may also alter the observed effect of plant diversity. For example, simplified ecosystems such as agricultural systems – where we often see negative diversity-herbivory relationships (Andow 1991) – may be dominated by monophages, because monocultures on very large scales may discourage polyphages (or even many cladophages). Whereas polyphages need not be less common compared with monophages in monocultures that are imbedded in a more diverse landscape (as is the case for most biodiversity experiments), as long as the scale of the plots does not exceed the dispersal capability of the polyphages.

Conclusion

Here I have shown that incorporating measures of phylogenetic diversity can improve our understanding of the role of plant diversity in promoting or suppressing herbivore damage. Phylogenetic diversity was negatively correlated with herbivory in an old field

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

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

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

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

479 species richness.

480

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485

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487

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695

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).

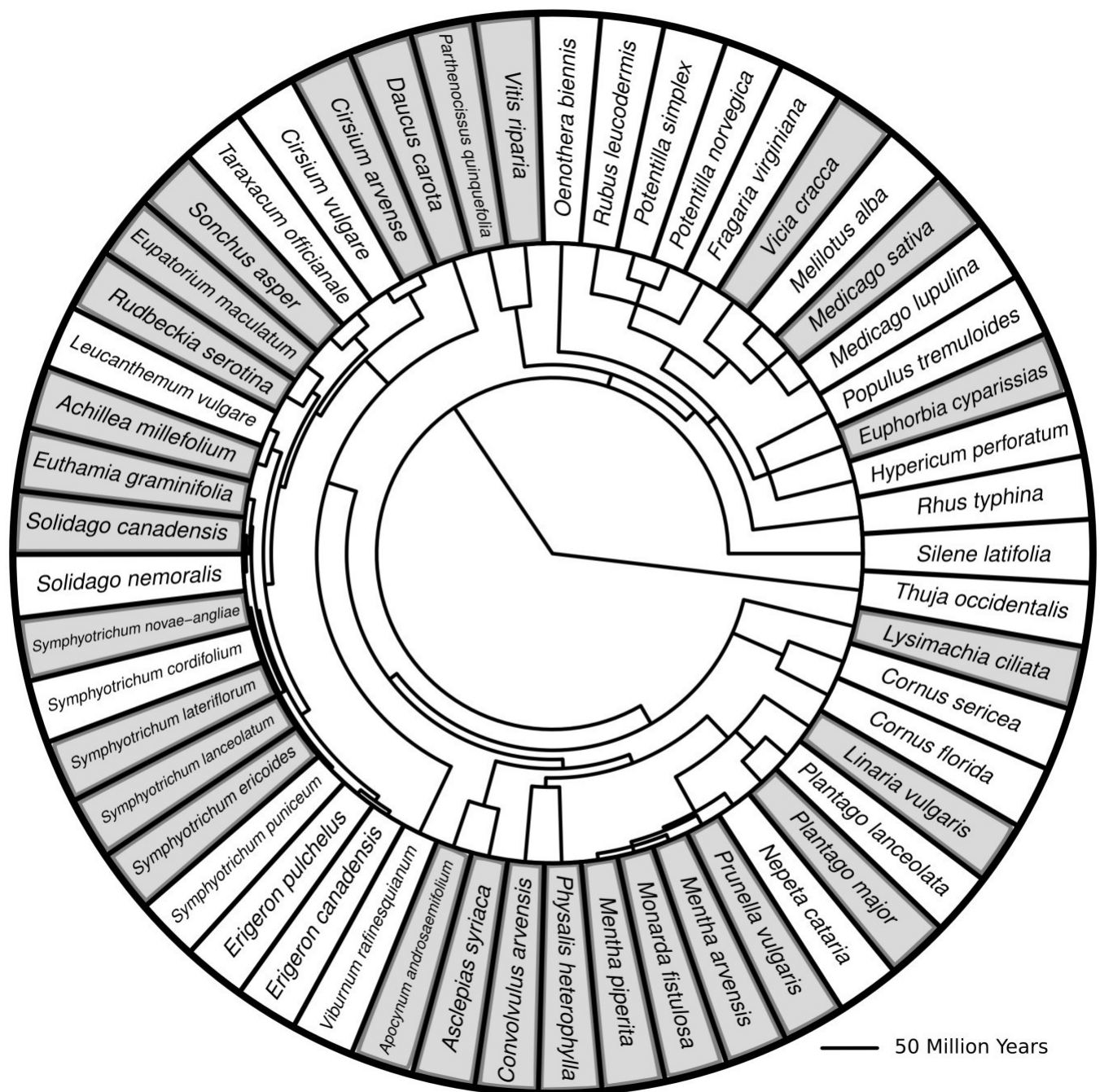
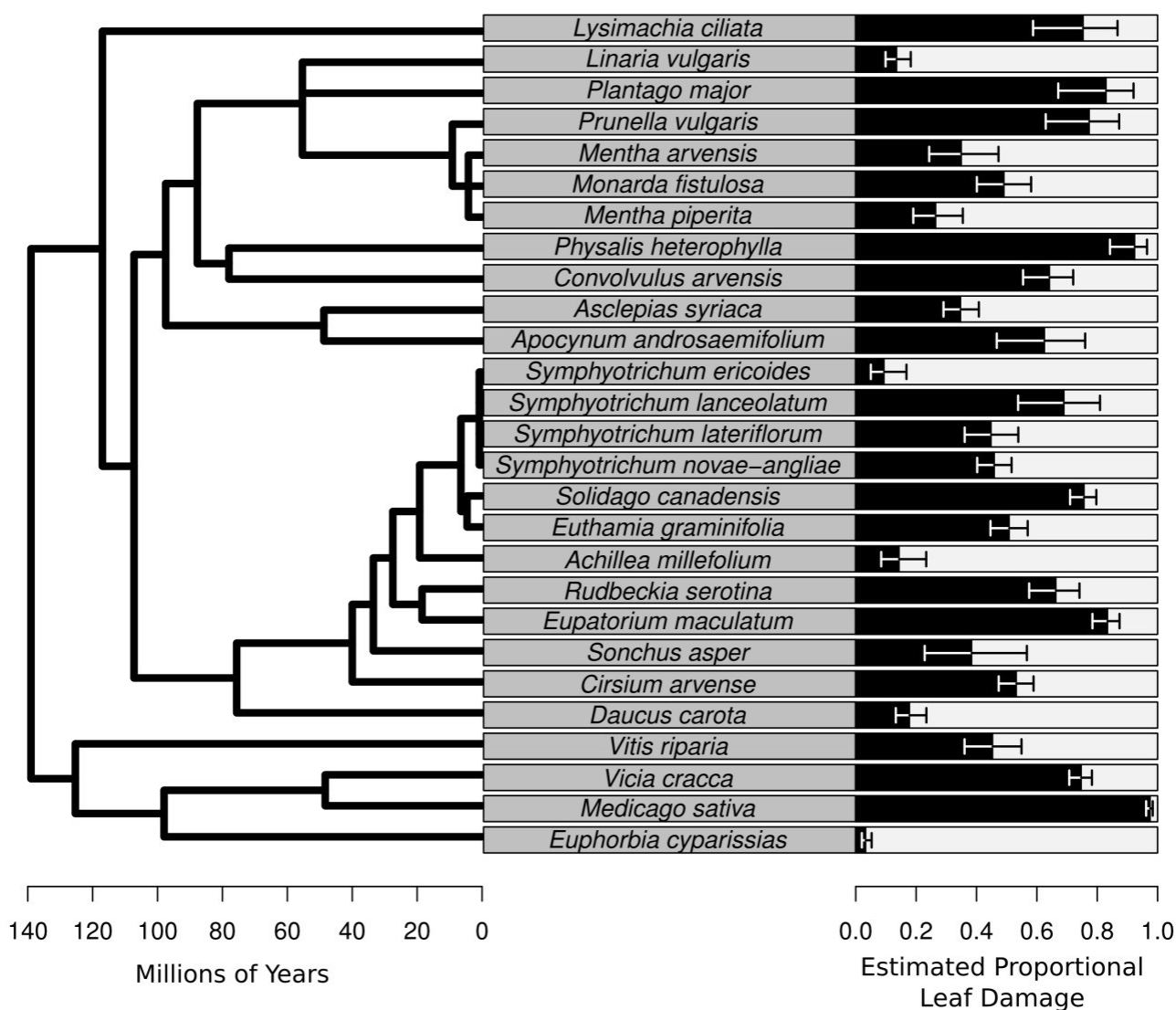



Figure 2

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.

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.