

Phylogenetic and taxonomic diversity interactively affect the functioning of
freshwater ecosystem

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Introduction

We are currently facing a massive biodiversity loss on Earth, which parallels big extinctions of the geological history of our planet (Barnosky et al., 2011). This biodiversity crisis poses key questions: what are the consequences of biodiversity loss for the functioning of ecosystems worldwide? Which ecosystems services will be most affected with the loss of species or functional richness (Loreau, 2010; Naem et al., 2012)? Historically, field experiments involving biodiversity and ecosystem functioning (BEF) have manipulated species and functional diversity of plants (reviewed in Loreau, 2010; Cardinale et al., 2011). Nonetheless, the way experimental treatments were built has been criticized on being too simplistic for not including vertical diversity (Duffy 2009).

Food web theory has only recently been incorporated into BEF experiments (Thebault and Loreau, 2003; 2006; Loreau, 2010), especially with freshwater systems (e.g., Cardinale et al., 2006; Duffy et al., 2007; Woodward, 2009). This arose from the need to add more realism into BEF experiments. Much of the theory on the effects of vertical diversity on EF suggest that difference in resource acquisition by animals and plants would produce complex results than experiments manipulating only single trophic levels (e.g., producers; Duffy et al. 2007). For example, trophic chain length is predicted to influence the likelihood of trophic cascades (Duffy et al. 2007) and indirect effects (Downing and Leibold 2002), which can influence density-dependent relationships between predators and prey, and biomass as a result. Also, prey edibility is thought to have a key role in mediating biodiversity effects related to selection effects, since it can change dominance patterns (Duffy et al. 2007). However, such experiments also manipulated species richness, assuming that species represented

independent entities and would be good proxies for the niche space occupied by a community (Tilman et al. 1997, Loreau 2010).

Concurrently, there is growing evidence that other facets of biodiversity, other than taxonomic and functional diversity, are involved in regulating ecosystem processes (e.g., Srivastava et al., 2012; Cadotte, 2013). Species traits represent the occupation of the niche space in a community and how efficiently resources are used. They are thought to be the primary factors mediating BEF relationships (Loreau, 2010). However, it is hard to define a priori which and how many effect traits are involved in ecosystem functioning. This task becomes even more challenging when dealing with multitrophic systems. The reasoning of using phylogenetic diversity (PD) as a predictor of ecosystem functioning is that it could be a better proxy for a set of unmeasured species traits, and then a better representation of trait space, given that those traits are correlated with the phylogeny, i.e., have a phylogenetic “signal” (Srivastava et al., 2012). In fact, recent studies with a single trophic level demonstrated that distant relatives could contribute more to plant biomass (a proxy for productivity) than recently diverged species pairs (Venail et al., 2008; Cadotte et al. 2008; Venail and Vives, 2013), due to increasing niche breadth and niche partitioning, resulting in more efficient use of available resources.

Conversely, there are some situations in which PD will not be a good predictor of ecosystem functioning. For example, when effect traits that drive a certain ecosystem functioning do not have phylogenetic signal at the community scale (Srivastava et al., 2012). Accordingly, the detection of phylogenetic signal also depends on the phylogenetic structure of the community (e.g., Graham et al., 2012), environmental harshness (Burns and Strauss, 2012), and scale (Kembel and Cahil, 2011). Thus, the detection of a phylogenetic signal in the regional phylogeny does not

guarantee that the same applies at the finer spatial scale of a community (Srivastava et al., 2012). Additionally, environmental conditions that do not favor strong trait conservatism (e.g., Burns and Strauss, 2012) or that promote strong selection due to interspecific competition (Gravel et al., 2012) may result in trait overdispersion, which undermine the effect of PD on EF.

Despite the amount of work accumulated in terrestrial ecosystems, in experiments manipulating richness and functional groups of grasses (reviewed in Cardinale et al., 2011), comparatively less work has been done in freshwater ecosystems (Petchey et al., 2002, Giller et al. 2004), especially involving multitrophic systems and measuring multiple ecosystem functions (Duffy et al., 2007, Woodward 2009). Furthermore, no study so far investigated the role of phylodiversity on the functioning of freshwater ecosystems with multiple trophic levels.

Here, we re-analyzed a dataset from an experiment that investigated the role species richness and composition of multitrophic freshwater communities on multiple ecosystem functioning (Downing and Leibold, 2002; 2010). Despite not designed explicitly to manipulate PD, this experiment offers an opportunity to investigate for the first time how well PD would predict ecosystem functioning in aquatic ecosystems with more than one trophic level.

Material and Methods

We re-analyzed the data from an experiment by Downing and Leibold (2002; 2010) that had three treatments with 3, 9, and 15 species, to which seven different species composition were nested, with a total of 21 different species composition. A phylogenetic tree for the species pool used in the experiment was built, consisting of 19 species (*Vallisneria americana* and *Utricularia vulgaris* were excluded since both

125 species died throughout the experiment; Downing and Leibold, 2002). A pseudo-
126 chronogram was then obtained with the BLADJ algorithm of the software Phylocom
127 4.2 (Webb et al., 2008) by interpolating nodes without known ages in between nodes
128 with known ages. Node ages were obtained from the web site <www.timetree.org>
129 (Kumar and Hedges, 2011). The algorithm then returned a dated tree with branch
130 lengths in millions of years (Fig. 1). The tree is more balanced than predicted by a
131 Yule (pure birth) model ($I_c=49$; $P=0.75$) and the nodes have a tendency to be closer to
132 the tips than the root (Pybus' $\gamma=0.44$; $P=0.656$).

133 Then, several phylogenetic diversity measures were calculated following
134 Cadotte (2013) to each of the 21 species composition manipulated in the experiment,
135 namely: PD, PSV, NMTD, H_{AED} , MPD, Simpson diversity, Shannon diversity, and
136 Rao diversity in R packages `picante` (Kembel et al., 2010) and `ecoPD` (Regetz et
137 al., 2009). PD, NMTD, and Simpson and Shannon diversities increase with increasing
138 species richness, whereas PSV, Rao, MPD and H_{AED} are independent of richness.

139 These phylogenetic diversity measures were used as predictors in hierarchical
140 linear mixed effect models in R package `lme4` (Bates et al., 2013) to predict each of
141 the ecosystem functioning originally measured (Downing and Leibold, 2002),
142 namely: productivity, respiration, and decomposition. To select the best random
143 effect, four models with intercepts for time, PD, and time + PD, and tank, with tank as
144 grouping variable were built. The model that included an intercept for only tank was
145 the best model. Then, eight models with different combinations of time, richness, and
146 PD as fixed effects, and a null model, with only the intercept as predictor were built.
147 These models were entered in a model selection procedure, to which the AIC_c , Akaike
148 weights (Burnham and Anderson, 2002), and the R^2_{pseudo} (Nakagawa et al., 2013) were
149 calculated. Model selection and R^2_{pseudo} were run in R packages `MuMIn` (Bartoń,

Diogo Provete 1/10/13 15:09

Comment [1]: I followed Cadotte (2013) and calculated all these indexes, but I only ran the analyses for PD and PSV. I'm not sure if I should run or not...

Diogo Provete 23/9/13 10:44

Comment [2]: I'm also not sure if I should run the models for plankton biomass.

2013) and `bbm1e` (Bolker, 2013). Phylogenetic diversity varied consistently among treatments (Fig. S1).

Results

The best model to explain productivity included the interaction between PD and species richness (Table 1), with strong support of all model selection measures. This result is similar even to the phylodiversity measure that is independent of species richness (Table S1). Decomposition was best explained simply by time when considering PD. Interestingly, both models with time and PSV + time appeared as the best models, with similar R^2_{pseudo} and AIC, but with the model including only time having slightly better Akaike weight. Results for respiration were similar to decomposition, with strong support for the model including only time, regardless of the phylodiversity measure.

Discussion

We found that phylodiversity was as good predictor as species richness for productivity, but not respiration. The results for decomposition showed a complex pattern. Overall, these results are similar to a previous meta-analysis of several experiments with grassland plants that did not explicitly manipulated PD (Cadotte et al., 2008), and a recent experiment that manipulated richness and PD of a single trophic level independently (Venail and Vives, 2013).

It is not clear what mechanisms are involved in the influence of evolutionary history on productivity, but previous studies with grassland plants have equated PD with niche differentiation and the complementarity effect (Venail et al. 2008; Cadotte 2013). Accordingly, a recent study (Turnbull et al. 2013) pointed out that, under some

175 circumstances, stabilizing niche differences could be related to the complementarity
176 effect (Loreau & Hector 2001). A previous study with grasses found a relatively
177 strong relationship between complementarity and PD (Cadotte 2013). For plants, this
178 is hypothesized to arise from the fact that close relatives have similar resource
179 requirements, increased likelihood for competition, and pathogen share (Loreau and
180 Hector 2001). There seems to be low support for selection effects as main drivers of
181 ecosystem functioning in the experiment by Downing and Leibold (2002), since the
182 effects of species are via indirect effects on other species. Therefore, it is tempting to
183 suggest that the relationship we found between PD and productivity, and respiration is
184 due to complimentary effects. Indeed, there seems to be some evidence showing that
185 distant-related species are more likely to exhibit niche segregation (Vamosi et al.
186 2009), potentially leading to a more efficient use of available resources and increased
187 productivity (Cadotte 2013). However, no study has provided unequivocal evidence
188 relating PD with complementary effects in complex, multitrophic systems.

189 PD seems not to be a good predictor of decomposition. Instead, our results
190 suggest that the model including only time was the best model, which contrasts with
191 the results of Downing & Leibold (2002), who found an effect of species composition
192 on decomposition. It is possible that effect traits relevant for decomposition are under
193 stabilizing selection and are best modeled by other models of evolution (e.g.,
194 Ornstein-Uhlenbeck), instead of a Brownian Motion model, on which a simple
195 measure of phylogenetic distance (PD) is based (see Mouquet et al., 2012; Gravel et
196 al. 2012). An alternative explanation involves the bacterial community composition in
197 the treatments, which could be potentially be involved in the decomposition process,
198 as already mentioned by Downing & Leibold (2002). Therefore, this result builds up
199 on previous studies (e.g., Gravel et al. 2012, Jabiol et al. 2013) claiming that in order

200 to have a comprehensive understanding of the effect of evolutionary history on EF,
201 one needs to gather

202 We found that a richness-independent measure of phylodiversity (PSV) was
203 the best predictor for ecosystem respiration. AND I HAVE NO IDEA WHY!!
204 PLEASE, HELP, SOS, AYUDAME, M'AIDE

205 In conclusion, our results suggest that the phylogenetic history of an
206 assemblage can partially help understand the relationship between biodiversity and
207 freshwater ecosystem functioning. However, much remains to be done to uncover the
208 mechanism driving the relationship between phylodiversity and ecosystem
209 functioning. For example, effect traits and those related to dominance need to be
210 analyzed in conjunction with the phylogeny, in order to test how they evolved along
211 the phylogeny and how these patterns influence their effects on ecosystem
212 functioning.

213

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222

223 **References**

224 Barnosky AD, Matzke N, Tomiya S et al (2011) Has the Earth's sixth mass extinction
 225 already arrived? *Nature* 471: 51-57.

226 Bartoń K (2013) MuMIn: Multi-model inference. R package version 1.9.5.
 227 <http://CRAN.R-project.org/package=MuMIn>

228 Bates D, Maechler M, Bolker B, Walker S (2013) lme4: Linear mixed-effects models
 229 using S4 classes. R package version 1.0-4. [http://CRAN.R-](http://CRAN.R-project.org/package=lme4)
 230 [project.org/package=lme4](http://CRAN.R-project.org/package=lme4)

231 Bolker B, R Development Core Team (2013) bbmle: Tools for general maximum
 232 likelihood estimation. R package version 1.0.13. [http://CRAN.R-](http://CRAN.R-project.org/package=bbmle)
 233 [project.org/package=bbmle](http://CRAN.R-project.org/package=bbmle)

234 Burnham KP and Anderson DR (2002) Model selection and multimodel inference: a
 235 practical information-theoretic approach. 2ed., Springer, New York.

236 Cadotte MW (2013) Experimental evidence that evolutionarily diverse assemblages
 237 result in higher productivity. *Proc Natl Acad Sci USA* 110: 8996-9000.

238 Cadotte MW, Cardinale BJ, Oakley TH (2008) Evolutionary history and the effect of
 239 biodiversity on plant productivity. *Proc Natl Acad Sci USA* 105: 17012-7.

240 Cadotte MW, Cavender-Bares J, Tilman D, Oakley TH (2009) Using phylogenetic,
 241 functional and trait diversity to understand patterns of plant community
 242 productivity. *Plos one* 4: e5695.

243 Cardinale BJ, Srivastava DS, Duffy EJ et al (2006) Effects of biodiversity on the
 244 functioning of trophic groups and ecosystems. *Nature* 443: 989-92.

245 Downing AL, Leibold MA (2002) Ecosystem consequences of species richness and
 246 composition in pond food webs. *Nature* 416: 837-841.

247 Downing AL, Leibold MA (2010) Species richness facilitates ecosystem resilience in
 248 aquatic food webs. *Freshwater Biol* 55: 2123-2137.

249 Duffy JE (2009) Why biodiversity is important to the functioning of real-world
 250 ecosystems. *Front Ecol Environ* 7: 437-44.
 251 Duffy JE, Cardinale BJ, France KE et al (2007) The functional role of biodiversity in
 252 ecosystems: incorporating trophic complexity. *Ecol Let* 10: 522-38.
 253 Faith DP (1992) Conservation evaluation and phylogenetic diversity. *Biol Conserv*
 254 61: 1-10.
 255 Giller PS, Hillebrand H, Berninger U-G et al (2004) Biodiversity effects on ecosystem
 256 functioning: emerging issues and their experimental test in aquatic environments.
 257 *Oikos* 104: 423-36.
 258 Gravel D, Bell T, Barbera C et al (2012) Phylogenetic constraints on ecosystem
 259 functioning. *Nat Commun* 3: 1117.
 260 Kembel SW, Cowan PD, Helmus MR et al (2010) Picante: R tools for integrating
 261 phylogenies and ecology. *Bioinformatics* 26:1463-1464.
 262 Kumar S, Hedges SB (2011) TimeTree2: species divergence times on the iPhone.
 263 *Bioinformatics* 27: 2023-4.
 264 Jabiol J, McKie BG, Bruder A et al (2013) Trophic complexity enhances ecosystem
 265 functioning in an aquatic detritus-based model system. *J Anim Ecol* doi:
 266 10.1111/1365-2656.12079
 267 Loreau M (2010) From populations to ecosystems: theoretical foundations for a new
 268 ecological synthesis. Princeton Univ Press, Princeton.
 269 Mouquet N, Devictor V, Meynard CN et al (2012) Ecophylogenetics: advances and
 270 perspectives. *Biol Rev* 87: 769-85.
 271 Naeem S, Duffy JE, Zavaleta E (2012) The Functions of Biological Diversity in an
 272 Age of Extinction. *Science* 336: 1401-6.

273 Nakagawa S, Schielzeth H, O'Hara RB (2013) A general and simple method for
 274 obtaining R² from generalized linear mixed-effects models. *Methods Ecol Evol* 4:
 275 133-42.

276 Petchey OL, Morin PJ, Hulot F et al (2002) Contribution of aquatic model systems to
 277 our understanding of biodiversity and ecosystem functioning. In: Loreau M,
 278 Naeem S, Inchausti P (eds) *Biodiversity and Ecosystem Functioning: Synthesis*
 279 *and Perspectives*. Oxford university press, Oxford, pp 127-138.

280 Regetz J., Cadotte M. Davies J (2009). ecoPD: Ecologically-informed phylodiversity
 281 metrics. R package version 0.2/r94. <http://R-Forge.R-project.org/projects/ecopd/>

282 Srivastava DS, Cadotte MW, MacDonald AA et al (2012) Phylogenetic diversity and
 283 the functioning of ecosystems. *Ecol Lett* 15: 637-648.

284 Thébault E, Loreau M (2003) Food-web constraints on biodiversity and ecosystem
 285 functioning relationships. *Proc Natl Acad Sci USA* 100: 14949-54.

286 Thebault E, Loreau M (2006) The relationship between biodiversity and ecosystem
 287 functioning in food webs. *Ecol Res* 21: 17-25.

288 Turnbull LA, Levine JM, Loreau M, Hector A (2013) Coexistence, niches and
 289 biodiversity effects on ecosystem functioning. *Ecol Lett* 16 Suppl 1: 116-27.

290 Webb CO, Ackerly DD, Kembel SW (2008) Phylocom: software for the analysis of
 291 phylogenetic community structure and trait evolution. *Bioinformatics* 24: 2098-
 292 100.

293 Woodward G (2009) Biodiversity, ecosystem functioning and food webs in fresh
 294 waters: assembling the jigsaw puzzle. *Freshwater Biol* 54: 2171-87.

296 **Figure legends**

297

298 Figure 1. Pseudo-chronogram assembled for the species used in the Downing and
299 Leibold's (2002) experiment, showing the nodes (black dots) with known ages used to
300 calibrate the chronogram.

301

302 **Table legends**

303

304 Table 1. Model selection results for productivity using different combinations of PD,
305 time, and diversity as predictors. ΔAIC is the difference between the best model and
306 the remaining. $w_i AICc$ is the Akaike weights.

307

308 Table 2. Model selection results for decomposition using different combinations of
309 PD, time, and diversity as predictors. ΔAIC is the difference between the best model
310 and the remaining. $w_i AICc$ is the Akaike weights.

311

312 Table 3. Model selection results for respiration using different combinations of PD,
313 time, and diversity as predictors. ΔAIC is the difference between the best model and
314 the remaining. $w_i AICc$ is the Akaike weights.

315

316 **Supplementary material**

317

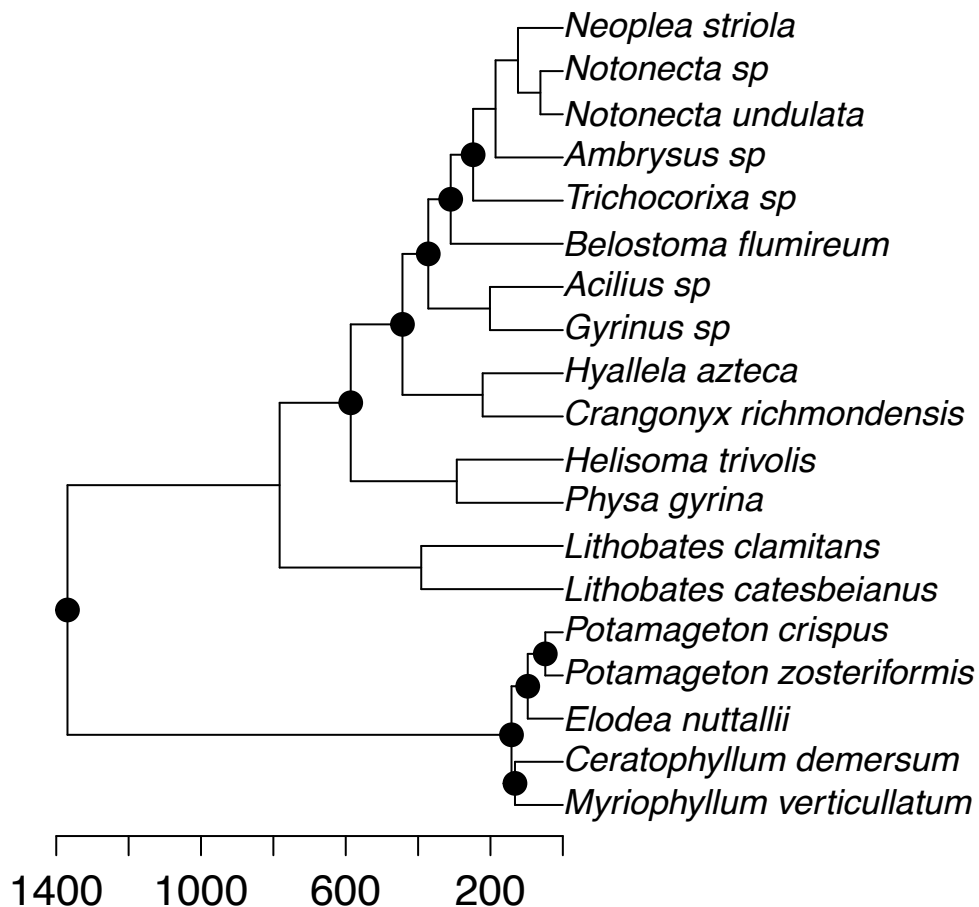
318 Table S1. Model selection results for productivity using different combinations of
319 PSV, time, and diversity as predictors. ΔAIC is the difference between the best model
320 and the remaining. $w_i AICc$ is the Akaike weights.

321

322 Table S2. Model selection results for decomposition using different combinations of
323 PD, time, and diversity as predictors. ΔAIC is the difference between the best model
324 and the remaining. $w_i AICc$ is the Akaike weights.

325

326 Table S3. Model selection results for respiration using different combinations of PD,
327 time, and diversity as predictors. ΔAIC is the difference between the best model and
328 the remaining. $w_i AICc$ is the Akaike weights.



Models for Productivity	k	ΔAICc	$w_i\text{AIC}$	R^2_{Pseudo}
PSV*diversity	8	0	0.985	0.02
PSV + diversity	6	10.7	0.004	0.02
PSV	7	10.8	0.004	0.001
Diversity	5	12.8	0.001	0.01
Intercept	3	12.9	0.001	-
PSV+ diversity + time	4	14.5	<0.001	0.02
PSV + time	5	14.6	<0.001	0.001
Diversity + time	4	16.6	<0.001	0.01
time	5	16.6	<0.001	<0.001

Models for Decomposition	k	ΔAICc	$w_i\text{AICc}$	R^2_{Pseudo}
time	4	0	0.542	0.32
PSV + time	5	0.4	0.445	0.33
Diversity + time	6	8.8	0.006	0.33
PSV+ diversity + time	7	9.0	0.006	0.33
Intercept	3	121.7	<0.001	-
PSV	4	122.1	<0.001	0.08
PSV*diversity	8	126.8	<0.001	0.09
Diversity	5	130.5	<0.001	0.09
PSV + diversity	6	130.7	<0.001	0.09

Models for Respiration	k	ΔAICc	$w_i\text{AIC}$	R^2_{pseudo}
time	4	0	0.958	0.52
PSV + time	5	6.4	0.039	0.52
Diversity + time	6	12.5	0.001	0.52
PSV + time + Diversity	7	19.7	<0.001	0.52
intercept	3	275.9	<0.001	-
PSV	4	282.3	<0.001	0.04
Diversity	5	288.6	<0.001	0.04
PSV + Diversity	6	295.9	<0.001	0.04
PSV * Diversity	8	300.4	<0.001	0.05

Models for Respiration	k	ΔAICc	$w_i\text{AIC}$	Pseudo R^2
time	4	0	0.971	0.52
PD + time	5	7.2	0.026	0.52
Diversity + time	6	12.5	0.001	0.52
PD + time + Diversity	7	23.2	<0.001	0.52
intercept	3	275.9	<0.001	-
PD	4	283.1	<0.001	0.04
Diversity	5	288.6	<0.001	0.04
PD + Diversity	6	299.3	<0.001	0.04
PD * Diversity	8	316.6	<0.001	0.05

Models for Decomposition	k	ΔAICc	$w_i\text{AIC}$	Pseudo R^2
time	4	0	0.948	0.32
PD + time	5	6.4	0.039	0.33
diversity + time	6	8.8	0.011	0.33
PD + time + diversity	7	13.6	0.001	0.33
Intercept	3	121.7	<0.001	-
PD	4	128.1	<0.001	0.08
diversity	5	130.5	<0.001	0.09
PD + diversity	6	135.3	<0.001	0.09
PD * diversity	8	139.3	<0.001	0.09

Models for Productivity	k	ΔAICc	$w_i\text{AIC}$	R^2_{Pseudo}
PD * diversity	8	0	1	0.99
PD + factor(div)	6	3506.7	<0.001	0.05
PD + time + factor(div)	7	3510.5	<0.001	0.05
factor(div)	5	3513.5	<0.001	0.01
Intercept	3	3513.5	<0.001	-
PD	4	3516.4	<0.001	0.001
factor(div) + time	6	3517.2	<0.001	0.01
time	4	3517.3	<0.001	<0.001
PD + time	5	3520.1	<0.001	0.001

Total Species Pool = 21 spp

Experimental pond =
sampling unit
Total of ponds = 84

