

2 **Global biodiversity, stoichiometry and ecosystem function responses to human-**  
3 **induced C-N-P imbalances.**

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27 **Abstract**

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29 Global change analyses usually consider biodiversity as a global asset that needs to be  
30 preserved. Biodiversity is frequently analysed mainly as a response variable affected by  
31 diverse environmental drivers. However, recent studies highlight that gradients of  
32 biodiversity are associated with gradual changes in the distribution of key dominant  
33 functional groups characterized by distinctive traits and stoichiometry, which in turn  
34 often define the rates of ecosystem processes and nutrient cycling. Moreover, pervasive  
35 links have been reported between biodiversity, food web structure, ecosystem function  
36 and species stoichiometry. Here we review current global stoichiometric gradients and  
37 how future distributional shifts in key functional groups may in turn influence basic  
38 ecosystem functions (production, nutrient cycling, decomposition) and therefore could  
39 exert a feed-back effect on stoichiometric gradients. The C-N-P stoichiometry of most  
40 primary producers (phytoplankton, algae, plants) has been linked to functional trait  
41 continua (i.e. to major axes of phenotypic variation observed in inter-specific analyses  
42 of multiple traits). In contrast, the C-N-P stoichiometry of higher-level consumers  
43 remains less precisely quantified in many taxonomic groups. We show that significant  
44 links are observed between trait continua across trophic levels. In spite of recent  
45 advances, the future reciprocal feedbacks between key functional groups, biodiversity  
46 and ecosystem functions remain largely uncertain. The reported evidence, however,  
47 highlights the key role of stoichiometric traits and suggests the need of a progressive  
48 shift towards an ecosystemic and stoichiometric perspective in global biodiversity  
49 analyses.

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51 Key words: stoichiometry, biodiversity, species richness, ecosystem function

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54 **Introduction: Global changes in biodiversity and Earth system stoichiometry**

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56 During the last centuries human activities have significantly altered both global  
57 biodiversity patterns and nutrient cycling, increasing the availability of nitrogen and  
58 carbon in the biosphere and causing widespread biodiversity declines (Rockström et al.,  
59 2009; Elser et al., 2009; Butchart et al., 2010; Erisman et al., 2013). Critically, the  
60 ongoing human-induced increases in carbon and nitrogen are not paralleled by a  
61 proportional increase in phosphorus input. As a result, these changes are producing an  
62 unprecedented human-induced imbalance between C- N- and P stoichiometry in earth's  
63 life system (Peñuelas et al., 2012, 2013a). Here we analyse how increased C-N-P  
64 imbalances in the earth system may alter global biodiversity patterns and their effect on  
65 ecosystem functions.

66 Fossil fuel combustion and crop fertilization have changed the global nitrogen  
67 cycle, leading to a significant increase in atmospheric N deposition at the global scale  
68 (Vitousek et al., 1997; Rockström et al., 2009; Canfield et al., 2010; Peñuelas et al.,  
69 2013a). N inputs of anthropogenic origin into the Biosphere have been estimated in  
70  $165\text{-}259 \text{ Tg N yr}^{-1}$ . Notably, this quantity is roughly equivalent to the total amount of N  
71 fixed in the biosphere by natural processes (Elser et al., 2009; Peñuelas et al., 2012,  
72 2013a). Due to the continuous anthropogenic inputs of N into the system, atmospheric  
73 N deposition has continuously increased from  $32 \text{ Tg N yr}^{-1}$  in 1860 to the current levels  
74 of  $112\text{-}116 \text{ Tg yr}^{-1}$  (Peñuelas et al., 2012, 2013a). Both reduced and oxygenated forms  
75 of inorganic N in the atmosphere are continuously introduced in terrestrial ecosystems,  
76 mainly through dry deposition, wet deposition or cloud water deposition processes

77 (Throop and Lerdau, 2004; Elser et al., 2009). Generally, the concentrations in N  
78 deposition of the reduced ( $\text{NH}_x$ ) and oxygenated ( $\text{NO}_y$ ) forms usually depend on the  
79 relative importance of agricultural and fossil fuel combustion activities at the regional  
80 scale (Throop and Lerdau, 2004; Sutton et al., 2007).

81 Human-induced imbalances on environmental C-N-P stoichiometry can impact  
82 biodiversity through multiple processes, including fertilization, eutrophication and  
83 acidification of terrestrial and aquatic ecosystems, increasing susceptibility to pests and  
84 environmental stresses, altering competitive and mutualistic relationships or by causing  
85 direct toxic effects on plants (Johnson, 1993; Olsson and Tyler, 2004; Elser et al., 2009;  
86 Bobbink et al., 2010; Stevens et al., 2010; Payne et al., 2013). For example, in the case  
87 of terrestrial plants increased ammonium availability can be toxic and cause very poor  
88 root and shoot development, especially in habitats with nitrate as the dominant N form  
89 (Bobbink et al., 2010). Likewise, the deposition of nitric acid frequently alters soil  
90 chemistry and leads to the depletion of essential cations (Mg, Ca, K) and can decrease  
91 soil pH and mobilize aluminum (Al) into the soil solution (Throop and Lerdau, 2004;  
92 Bobbink et al., 2010). Soil acidification in turn reduces biodiversity by producing  
93 toxicity effects due to exceedance of biological thresholds to soil pH and due to the  
94 release of toxic ions such as  $\text{Al}^{3+}$  (Bobbink et al., 2010; Jones et al., 2014). Similarly,  
95 the rates of N mineralization and nitrification tend to increase with N deposition  
96 (Throop and Lerdau 2004), but mineralization rates can also decline after soils become  
97 N saturated leading to reduced nitrification and promoting the accumulation of litter  
98 (Throop and Lerdau, 2004; Bobbink et al., 2010; Jones et al., 2014). N deposition can  
99 result in both reduced demographic performance of plants and reduced resistance to  
100 pathogens and insect pests, and can also in turn increase leaf N content and promote  
101 herbivory (Bobbink et al., 2010). Moreover, N deposition can alter shoot/root ratios and

102 influence the susceptibility of plants to drought and frost (Bobbink et al., 2010). Finally,  
103 changes on soil pH also influence P availability and affect plant growth (Kooijman et  
104 al., 1998; Jones et al., 2014). In sum, the available evidence highlights that multiple  
105 ecological processes have been largely impacted by increased N deposition rates and  
106 growing C-N-P imbalances.

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108 High levels of nitrogen deposition have been reported mainly on terrestrial soils  
109 and lakes in densely populated areas of the Northern Hemisphere and several populated  
110 coasts across the globe (e.g. China, South America, North Atlantic and Baltic Sea  
111 coasts), causing important declines in biodiversity in these areas (Bobbink et al., 2010;  
112 Stevens et al., 2010; Kim et al., 2011; Payne et al., 2013). In contrast, phosphorus  
113 deposition, mainly caused by mineral aerosols (e.g. dust and wildfire ashes) but also by  
114 anthropogenic combustion that seems now to represent 30% of the global atmospheric P  
115 source (Wang et al., 2014), has been globally quantified in about 3-4 Tg P yr<sup>-1</sup> (Wang  
116 et al., 2014). These quantities are roughly one order of magnitude smaller than global  
117 nitrogen deposition. Phosphorus fertilizers are less volatile and are not widely  
118 distributed by large-scale deposition processes, being mainly transported to nearby  
119 ecosystems after their application (Peñuelas et al., 2013a). Therefore, major phosphorus  
120 fertilizer impacts have been mainly concentrated in some estuarine areas and in soils  
121 and streams located nearby intensively fertilized areas (Peñuelas et al., 2009, 2013a).

122 During the XXI century current high levels of nitrogen deposition in populated  
123 temperate regions of the Northern Hemisphere are expected to expand into tropical  
124 regions (Peñuelas et al., 2013a). Tilman et al. (2001) predicted a further 2.4- to 2.7-fold  
125 increase in agriculturally driven eutrophication with N and P by the year 2050. These  
126 global changes in N and P availability and in N:P ratio could alter the capacity of the

127 biosphere to fix carbon and global nutrient cycling dynamics (Hessen et al., 2004). By  
128 the end of the 21<sup>st</sup> century, for example, recent biogeochemical modelling analyses  
129 suggest, that phosphorus and nitrogen availability could still limit the projected increase  
130 in carbon storage in response to increasing atmospheric CO<sub>2</sub> concentrations (Peñuelas et  
131 al., 2013).

132         The reported increased C-N-P imbalances are promoting shifts on both terrestrial  
133 and marine biodiversity (Bobbink et al., 2010; Peñuelas et al., 2012, 2013a). However,  
134 it is important to bear in mind that biodiversity gradients are tightly associated with  
135 changes in the spatial distribution of major functional groups (e.g. Carnicer and Díaz-  
136 Delgado 2008; Kissling et al., 2011; Weber and Deutch 2010; Stefanescu et al., 2011;  
137 Carnicer et al., 2013; Coll et al., 2013; Barton et al., 2013; Carnicer et al., 2014a).  
138 Crucially, these groups have contrasting stoichiometric and functional traits, and may in  
139 turn influence the rates of ecosystem processes and nutrient cycling, therefore  
140 producing reciprocal feedbacks among biodiversity composition, stoichiometry and  
141 ecosystem dynamics (Hessen et al., 2004; Weber and Deutch, 2010, 2012). Nowadays,  
142 a large number of studies highlight the need to account for the interactions between  
143 biodiversity, species' functional traits, stoichiometry, nutrient cycling dynamics and  
144 ecosystem functions (Schulze and Mooney 1993; Naeem et al., 1994, 1995, 2009;  
145 Tilman 1997; Chapin et al., 2000; Kinzig et al., 2001; Hessen et al., 2004; Hooper et al.,  
146 2005; Loreau 2010; Butchart et al., 2010; Carnicer et al., 2012; Barton et al., 2013;  
147 Erisman et al., 2013). Moreover, evolutionary processes and phenotypically plastic  
148 responses need to be integrated also in the study of coupled feedbacks between  
149 biodiversity, nutrient cycling dynamics and global C-N-P imbalances (e.g. Elser et al.,  
150 2000b). To effectively integrate stoichiometry in global biodiversity analyses, the  
151 quantification of stoichiometric traits across several taxonomic and trophic groups will

152 be possibly required. Although major axes of stoichiometric variation have been  
153 quantified in some groups like plants, marine bacteria and phytoplankton (Wright et al.,  
154 2004; Litchman and Klausmeier, 2008; Lauro et al., 2009; Reich, 2014), we still lack a  
155 precise description of the patterns of variation in stoichiometric traits in other  
156 taxonomic groups.

157         The consequences of increased C-N-P imbalances on the reciprocal feedbacks  
158 between biodiversity, ecosystem properties and nutrient cycling remain, though, largely  
159 uncertain. To explore how increased C-N-P imbalances in the earth system may alter  
160 global biodiversity, we develop the following objectives: 1) to briefly enumerate and  
161 overview the main hypotheses explaining inter-specific differences in C-N-P content; 2)  
162 to synthesize the major axes of variation observed in inter-specific comparisons of  
163 stoichiometric and functional traits in diverse taxonomic groups; 3) to review the  
164 global-scale gradients in C-N-P stoichiometry of major taxonomic and functional  
165 groups and explore how they may evolve in response to major global change drivers;  
166 and 4) to analyse the major interactions between biodiversity and ecosystem functions  
167 that may occur in the face of the increased C-N-P imbalances. Below we devote a  
168 section each to these four objectives.

169

## 170 **1. Biodiversity and inter-specific differences in C-N-P content.**

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172 The impacts of increased global C-N-P imbalances on biodiversity will depend on the  
173 specific traits of each taxon (Elser et al., 1996; Hessen et al., 2004; Carnicer et al.,  
174 2012). For example, variation in species' C-N-P stoichiometry has been significantly  
175 linked to organism growth rate (Elser et al., 1996; Sterner and Elser, 2002), body mass  
176 and allometry (Elser et al., 1996; Vanni et al., 2002; Woods et al., 2003, 2004; Mulder

177 and Elser, 2009), taxonomic, phylogenetic and trophic group (Fagan et al., 2002;  
178 Hambäck et al., 2009; González et al., 2011), ontogenetic stage (Elser et al., 1996;  
179 Sterner and Elser, 2002), environment seasonality and the associated demand for  
180 storage in life history style (Hood and Sterner, 2010), investments in reproduction  
181 (Ventura and Catalan, 2005; Fujita et al., 2013), structural tissues and differential tissue  
182 allocation (Elser et al., 1996; Vanni et al., 2002; Woods et al., 2004; González et al.,  
183 2011) and genome and cell size (Hessen et al., 2010) (Table 1). Apart from all these  
184 species-specific factors, environmental factors also co-determine species stoichiometry.  
185 These environmental factors are diverse and include temperature (Woods et al., 2003;  
186 Reich and Oleksyn, 2004; Sun et al., 2013), substrate age (Walker and Syers, 1976;  
187 Reich and Oleksyn, 2004) and resource stoichiometry (Woods et al., 2002; Schade et al.,  
188 2003; Hessen et al., 2004; Small and Pringle, 2010). Overall, the available evidence  
189 supports that species-specific C-N-P stoichiometry is determined by multiple traits and  
190 environmental factors (Table 1). In spite of this overwhelming complexity of factors,  
191 both experimental and theoretical evidence suggests that species are adapted to species-  
192 specific optimal environmental C-N-P ratios (reviewed in Ågren et al., 2012).

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## 194 **2. Trait continua, stoichiometry and major inter-specific axes of phenotypic** 195 **variation**

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197 Diverse stoichiometric and life history traits have been measured across many species  
198 allowing comparative approaches at the inter-specific level. These analyses revealed the  
199 existence of adaptive trait continua, that is, suites of traits that tend to co-vary along a  
200 main axis of variation at the inter-specific level in plants (Grime et al., 1997; Wright et  
201 al., 2004; Chave et al., 2009; Peñuelas et al., 2010; Donovan et al., 2011; Carnicer et al.,



202 2014b), mammals (Bielby et al., 2007), birds (Sæther et al., 2011), fishes (Jeschke and  
203 Kokko, 2009), phytoplankton (Litchman and Klausmeier, 2008), marine bacteria (Lauro  
204 et al., 2009) and butterflies (Carnicer et al., 2012, 2013a). These continua often range  
205 from specialized to more generalist species and/or from slow to fast life strategies  
206 (Wright *et al.*, 2004; Bielby *et al.*, 2007; Sæther *et al.*, 2011; Carnicer et al. 2012,  
207 2013a). Trait continua quantify and summarize life history, functional trait and  
208 stoichiometric variation at the inter-specific level in multi-specific assemblages. It has  
209 been suggested that the mechanistic origin of these taxon-specific trait continua may  
210 rely on the evolutionary emergence of contrasting stoichiometric and life-history  
211 strategies that, in particular ecological contexts, maximize fitness by acquiring a  
212 different set of traits allowing for sustained population performance (Carnicer et al  
213 2012, 2013a). Therefore, trait continua synthesise the observed phenotypic space for a  
214 given taxonomic group in local, regional or global assemblages.

215         The variation in stoichiometric traits along these major functional trait axes (i.e.  
216 variation of C-N-P tissue content, C/N/P ratios) is relatively well described in some  
217 groups like plants (Wright et al., 2004; Reich, 2014), marine bacteria (Lauro *et al.*,  
218 2009) and some groups of phytoplankton (Litchman and Klausmeier, 2008). In contrast,  
219 for many terrestrial heterotroph groups (e.g. primary consumers, predators and  
220 detritivores) the inter-specific variation in C-N-P tissue content remains yet poorly  
221 quantified (but see Fagan et al., 2002; Denno and Fagan, 2003; Fagan and Denno, 2004;  
222 Woods et al., 2003, 2004; Martinson et al., 2008; Mulder and Elser, 2009; Bishop et al.,  
223 2010; Hämbäck et al., 2009; González et al., 2011; Lemoine et al., 2014). As a general  
224 rule, available studies suggest that there is a significant decrease in P content with body  
225 size in most heterotroph groups (Woods et al., 2004; Hämbäck et al., 2009; González et  
226 al., 2011). In addition, contrasting N, P values have been reported between primary

227 consumers and higher trophic levels in some taxonomic groups (Fagan et al., 2002;  
228 González et al., 2011; but see Woods et al., 2004). Likewise, significant differences in  
229 body N and P contents are observed between major insect orders. For example,  
230 Lepidoptera show the highest potential for P limitation because they have the lowest N  
231 and highest P concentrations when compared with other insect orders (Fagan et al.,  
232 2002; Woods et al., 2004). P limitation significantly affects many aspects of insect  
233 performance, like survival, development, growth rate, body size and sexual and  
234 oviposition behavior (reviewed in Tao and Hunter, 2012). In contrast, other orders such  
235 as Hemiptera are considered to be mainly N limited. Like in the case of phosphorus,  
236 nitrogen limitation often significantly determines insect demographic performance and  
237 improved performance of herbivorous insects has been observed after increased  
238 nitrogen deposition (Throop and Lerdau, 2004). This may be expected considering that  
239 insect body N concentrations are on average 10 times higher than those of their host  
240 plants (Tao and Hunter 2012). In addition, recent studies highlight that species-specific  
241 demands for nutrients and the defensive responses of host plants combine to determine  
242 the responses of herbivores to P availability under N deposition (Tao and Hunter 2012).  
243

244         Across multiple trophic levels, deciphering the relationships between major axes  
245 of variation in stoichiometric and functional traits emerges as a new reserach challenge.  
246 For example, a major axis of trait variation has been recently described in  
247 Mediterranean and temperate butterflies in Europe (Carnicer et al. 2012, 2013a;  
248 Dapporto and Dennis, 2013). In this group, traits and species-specific habitat measures  
249 covary along a main axis, ranging from multivoltine trophic generalists with high  
250 dispersal capacity to univoltine (i.e. one generation per year), trophic specialist species  
251 with low dispersal capacity (table 2). This trait continuum is closely associated with the

252 observed distributions of butterfly species along an altitudinal species richness gradient  
253 (Figure 1, and see Carnicer et al 2012, 2013a). In addition, the position of species along  
254 the trait continuum is significantly associated with inter-specific differences in patterns  
255 of spatial genetic variability ( $F_{ST}$  and genetic distances), population responses to the  
256 impacts of global change and local turnover dynamics (Figure 1, Carnicer et al 2012,  
257 2013a). However, the putative relationships of this trait continuum with stoichiometric  
258 traits in other trophic levels remains largely unexplored. As highlighted in Figure 2,  
259 major axes of phenotypic trait variation in butterflies can be significantly associated  
260 with leaf stoichiometric variation at lower trophic levels (host plants). Notably, leaf P  
261 and N concentration are two traits integrated in the leaf economics spectrum (Wright et  
262 al., 2004), a major axis of phenotypic variation between terrestrial plant species. Overall,  
263 Figure 2 illustrates that, across trophic levels, significant relationships hold between  
264 major life history axes (PCA 1) and stoichiometric traits (leaf N and P concentration).  
265 These results suggest that the consideration of stoichiometric and functional traits across  
266 multiple trophic levels might allow a better understanding of the structure, dynamics  
267 and stoichiometric constraints operating in plant-insect food webs.

268

### 269 **3. Global gradients in organism C-N-P stoichiometry**

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271 Large-scale gradients of both nutrient availability in the environment and organism C-  
272 N-P tissue concentration have been reported for several groups (Reich and Oleksyn,  
273 2004; Lambers et al., 2007, Sardans et al 2013, Daines et al 2014). For example,  
274 global-scale gradients in C-N-P tissue concentration and C-N-P ratios have been  
275 reported in plants, marine bacteria, phytoplankton, insects, mycorrhiza activity and  
276 plant litter (Reich and Oleksyn, 2004; Lambers et al., 2007; Manzoni et al., 2008; Sun

277 et al., 2013; Sardans et al., 2013; Daines et al., 2014). In marine ecosystems, lower  
278 organism N/P and C/P ratios are observed at high latitudes, in cold nutrient-rich  
279 environments, whereas higher C/N/P ratios dominate at low latitudes. High-latitude  
280 marine environments experience low temperatures and high nutrient concentrations, are  
281 often iron-limited and also experience seasonal blooms and limitation of phytoplankton  
282 growth by light availability (Weber and Deutch, 2010, 2012; Moore et al., 2013;  
283 Martiny et al., 2013; Daines et al., 2014). The opposite conditions (warm, oligotrophic,  
284 widespread N-limitation and P co-limitation in some localities) are generally observed  
285 at low latitudes and subtropical gyres. In contrast, equatorial regions are characterized  
286 by intermediate temperatures and nutrient concentrations due to upwelling processes  
287 (Martiny et al., 2013; Daines et al., 2014). These large-scale gradients in temperature  
288 and nutrient availability are in turn associated with gradients in species' stoichiometric  
289 values. For example, Martiny et al. (2013) reported C-N-P ratios of 195:28:1 in warm,  
290 nutrient-depleted low latitude gyres, 137:18:1 in warm, nutrient-rich upwelling zones  
291 and 78:13:1 in cold, nutrient rich high-latitude regions. The taxonomic composition of a  
292 community also significantly influences its elemental stoichiometry (Elser et al., 2000;  
293 Sterner and Elser, 2002). For example, communities dominated by diatoms have a lower  
294 N/P and C/P ratio and are more common in cold and nutrient-rich environments, located  
295 at high latitudes (Martiny et al., 2013). In contrast, communities located in subtropical  
296 oligotrophic gyres are dominated by N<sub>2</sub>-fixing cyanobacteria and other diazotrophs and,  
297 as a result, have higher C/P and N/P ratios and smaller sizes (Martiny et al., 2013;  
298 Barton et al., 2013). N/P ratios of phytoplankton show both significant differences  
299 between different phylogenetic groups and substantial intra-specific variation due to  
300 local acclimation and phenotypic plasticity (Weber and Deutch, 2010). In line with  
301 this, phytoplankton N/P ratios often depart from the Redfield ratio (16:1; Redfield,

302 1934), and observed inter-specific differences in N/P ratios span more than one order of  
303 magnitude (Weber and Deutch, 2010).

304         Several studies have analysed the stoichiometry of primary and secondary  
305 consumers in marine and freshwater food webs (Elser and Hassett, 1994; Dobberfuhl  
306 and Elser, 2000; Vanni et al., 2002). These studies report significant differences in C-N-  
307 P content between autotroph and heterotrophs that in turn influence nutrient recycling  
308 rates and productivity (Elser and Urabe, 1999; Vanni et al., 2002; Hessen et al., 2004).  
309 Herbivores tend to have higher N and P contents relative to C (Elser et al., 2000a).  
310 Stoichiometric differences between trophic levels are in turn associated with different  
311 stoichiometric plasticity between primary consumers (more plastic) and secondary  
312 consumers (less stoichiometric plasticity) (Hessen et al., 2004; Persson et al., 2010).  
313 Some pioneering studies have also quantified the stoichiometry of detritivore and  
314 benthic groups (Cross et al., 2003; Martinson et al., 2008; Alves et al., 2010).  
315 The future distribution of the diverse marine taxonomic, trophic and functional groups  
316 in the face of global change and increased C-N-P imbalance remain yet largely  
317 uncertain. Global change model projections for the oceans mostly predict greater  
318 stratification of the water column, weaker nutrient delivery to the surface and  
319 acidification (Sarmiento et al., 2004; Caldeira and Wickett, 2005; Barton et al., 2013).  
320 This may possibly expand the oligotrophic areas and facilitate the expansion of  
321 communities dominated by smaller phytoplankton, mainly dominated by N<sub>2</sub>-fixing  
322 cyanobacteria, other heterotrophic bacteria and generalist mixotrophs (bacteria that  
323 combine autotrophic and heterotrophic nutrition), small-sized zooplankton (Barton et al.,  
324 2013), and, if increased overfishing persists, gelatinous zooplankton (Richardson et al.,  
325 2009; Condon et al., 2012).

326

327 In the case of terrestrial plants, Reich and Oleksyn (2004) have reported a  
328 significant latitudinal increase in both leaf P and N concentration and a latitudinal  
329 decrease in N/P ratio. Similarly, Yuan et al (2011) reported latitudinal gradients for N  
330 and P in root tissues. Plant functional types (i.e. ruderals, stress-tolerants, competitive)  
331 significantly differ in their N, P concentration and N/P ratios (Grime, 1977). McJannet  
332 et al (1995) reported significant differences in N, P tissue concentration between plant  
333 functional strategies, with lower N, P and N/P ratios in ruderal species. Similarly,  
334 Willby et al (2001) reported that stress-tolerant plants (*S*) had consistently lower  
335 nutrient concentration and higher N/P ratios whereas ruderal plants (*R*) displayed the  
336 opposite pattern. Competitor (*C*) and competitor-stress tolerator plants (*CS*) were  
337 intermediate to *R* and *S*. In line with this, the abundance of the different functional types  
338 of plants and mycorrhizas varies along N/P gradients, and intermediate N/P ratios are  
339 associated with an increase of the number of different strategies that coexist (Lambers et  
340 al., 2007). As a result, species richness of herbaceous plants is usually higher at  
341 intermediate N/P ratios (Fujita et al., 2013). Low N/P ratio environments tend to favour  
342 ruderal plant types, fast growing species with long roots, and species associated with N  
343 fixers. Likewise, intermediate N/P ratios and high local productivity are often associated  
344 with a predominance of competitor plant types (Fujita et al., 2013). In other words,  
345 species with resource-acquisitive traits, such as high leaf N and P concentrations, high  
346 SLA and short leaf lifespan reach higher abundances or occur more frequently in sites  
347 with higher nutrient and/or water availability (Adler et al., 2013). Finally, oligotrophic  
348 and high N/P ratio environments favour slow-growing species, and stress-tolerant plant  
349 types (*S*) with specialized P uptake traits like cluster roots, arbuscular mycorrhizae or  
350 high phosphatase activity (Lambers et al., 2007; Fujita et al., 2013). For example, the  
351 numbers of stress-tolerant and endangered species is higher at high N/P ratios (Fujita et

352 al., 2013) and in low fertilized sites (Bobbink et al., 2010). These species are  
353 characterized by specific suites of traits, such as small investment in sexual  
354 reproduction, low seed number and seed investment, late start of flowering, short  
355 flowering period, perennial form, vegetative reproduction, low specific leaf area (SLA),  
356 high leaf dry matter content, low canopy height and low or absent association with N  
357 fixers. Crucially, plants can invest a high percentage of total phosphorus in reproduction  
358 (50-60%) (Fujita et al., 2013 and cites there in) and this results in significantly reduced  
359 investment in plant reproductive organs in phosphorus-limited environments with high  
360 N/P ratios (Fujita et al., 2013). In trees, deciduous species have higher leaf N and P than  
361 evergreens with similar leaf lifespan (Reich and Oleksyn, 2004). Deciduous trees make  
362 up a greater fraction of all species in temperate than in tropical zones thus contributing  
363 to higher leaf N and P in temperate forests (Reich and Oleksyn, 2004).

364         The response of plant functional groups to increased global C-N-P imbalance  
365 has been explored in diverse experimental studies (Silvertown et al., 2006; Bobbink et  
366 al., 2010). Available empirical evidence suggests different demographic responses  
367 between plant functional groups to increased imbalance in C-N-P supply. For example,  
368 long-term plant fertilization experiments report increases in the abundance of grasses,  
369 and significant reductions of the cover of legumes and broadleaved herbs (Silvertown,  
370 2006). Similarly, in a wide range of arctic, alpine and temperate ecosystems, lichens,  
371 mosses, and epiphytic species tend to be the most sensitive elements of ecosystems to  
372 increased N availability and deposition (reviewed in Bobbink et al., 2010). In contrast,  
373 in several terrestrial ecosystems grasses and sedges are often benefited from increased  
374 N deposition and altered C/N/P ratios (Bobbink et al., 2010).

375         In contrast to aquatic communities and terrestrial plant communities, large-scale  
376 gradients of N, P tissue concentration in terrestrial primary and secondary consumers

377 remain yet poorly quantified (Bertram et al., 2008; Hambäck et al., 2009; El-Sabaawi et  
378 al., 2012; Sun et al., 2013). The same applies to the stoichiometric differences in N, P  
379 concentration between major terrestrial groups of primary consumers, predators and  
380 detritivores (Fagan et al., 2002; Denno and Fagan, 2003; Woods et al., 2003, 2004;  
381 Martinson et al., 2008; Mulder and Elser, 2009; Bishop et al., 2010; Gónzalez et al.,  
382 2011; Lemoine et al., 2014).

383         In plants, aquatic communities, and secondary consumers the available empirical  
384 evidence suggests that several hypotheses jointly contribute to explain large-scale trends  
385 in N, P tissue content. Firstly, high nitrogen and phosphorus concentration may be  
386 adaptive at low temperatures (temperature–physiology hypothesis; Körner et al., 1986;  
387 Woods et al., 2003; Reich and Oleksyn, 2004; Table 1). Plants experimentally grown at  
388 low temperatures typically contain greater leaf N and P and this may be related to the  
389 diminished efficiency of N-rich enzymes and P-rich RNA at low temperatures (Reich  
390 and Oleksyn, 2004). The temperature-physiology hypothesis holds in diverse taxa,  
391 including both primary and secondary consumers (e.g. Woods et al. 2003, 2004, Reich  
392 and Oleksyn, 2004; Martiny et al., 2013). For example, cold-acclimated poikilotherms  
393 contain on average more nitrogen and phosphorus, protein and RNA than warm-  
394 acclimated conspecifics (Woods et al., 2003). Similarly, phytoplankton and plants show  
395 large-scale N-P gradients that have been significantly associated with spatial changes in  
396 ambient temperature (Reich and Oleksyn, 2004; Martiny et al., 2013). Secondly, large-  
397 scale gradients in N and P tissue content in terrestrial groups are also influenced by  
398 substrate age and fertility (Substrate age and substrate composition hypothesis, Reich  
399 and Oleksyn, 2004, Table 1). In terrestrial ecosystems tropical soils are on average older  
400 and more leached, and have lower fertility (Walker and Syers, 1976; Reich and Oleksyn,  
401 2004). Similarly, while in the Mediterranean biome the soils in South Africa and



402 Australia are geologically older and tend to be nutrient poor, in the Mediterranean basin,  
403 Chile and California soils often have higher nutrient contents (Ochoa-Hueso et al.,  
404 2011). Available evidence suggests that climate, substrate nutrient content and soil age  
405 gradients jointly contribute to the clinal variation of N and P content in organism tissues  
406 in several taxa (Reich and Oleksyn, 2004; Martiny et al., 2013). Moreover, mountain  
407 ranges and altitudinal gradients significantly influence soil nutrient content and regional  
408 variability in soil and organism tissue stoichiometry. For example, wet N deposition is  
409 often higher at high altitudes due to the increased importance of cloud water deposition,  
410 producing altitudinal gradients in N deposition (Bobbink et al., 2010). On the other  
411 hand, cold temperatures can slow down biogeochemical processes and result in  
412 decreased leaf N and P content at high latitudes (temperature–biogeochemistry  
413 hypothesis, Reich and Oleksyn, 2004). In addition, cold temperatures at high latitudes,  
414 such as arctic zones, can promote a dominance of  $\text{NH}_4^+$  over  $\text{NO}_3^-$  in soil  
415 biogeochemistry (Bobbink et al., 2010).

416 In spite of all this empirical evidence describing large-scale stoichiometric gradients,  
417 the patterns for many groups and elements remain unquantified and therefore unveiled,  
418 specially at higher trophic levels.

419

#### 420 **4- Biodiversity, ecosystem function and global unbalanced C-N-P stoichiometry.**

421

422 Substantial loss of species richness has been reported with increased N deposition and  
423 associated C-N-P imbalances in a wide range of habitats and taxa. For example, a  
424 decrease in plant richness has been observed in acid grasslands, sand dune and mixed  
425 grasslands, heath, bog, woodlands and forests (Stevens et al., 2004; Jones et al., 2004;  
426 2014; Maskell et al., 2010; Dupré et al., 2010; Bobbink et al. 2010; Ceulemans, 2013).

427 Similar trends have been observed in N-addition experiments, field surveys along N-  
428 deposition gradients and meta-analyses (Carroll et al., 2003; Stevens et al., 2004; Clark  
429 and Tilman, 2008; Dupré et al., 2010; De Schrijver et al., 2011; Isbell et al. 2013b).  
430 Crucially, a large number of studies now highlight an important role of biodiversity per  
431 se in determining basic ecosystem functions, such as productivity, nutrient cycling and  
432 decomposition rates. For example, studies highlight that loss of biodiversity can reduce  
433 biomass production efficiency, and alter nutrient cycling and decomposition rates  
434 (Tilman and Downing, 1994; Naeem et al., 1994; Tilman et al., 1996; Hector et al.,  
435 1999; Loreau et al., 2001; Reich et al., 2001; Loreau et al., 2001; Hooper et al., 2005;  
436 Cardinale et al., 2012; Reich et al., 2012). Moreover, other studies demonstrate that  
437 biodiversity can also increase the stability of ecosystem functions (Cardinale et al.,  
438 2006; Tilman et al., 2006; Hector and Bagchi, 2007; Zavaleta et al., 2010; Isbell et al.,  
439 2011; Cardinale et al., 2012; Reich et al., 2012; Sapijanskas et al., 2014). Several non-  
440 mutually exclusive mechanisms are possibly involved, for example recent studies show  
441 that biodiversity enhances ecosystem functioning by niche complementarity effects,  
442 compensatory dynamics associated with inter-specific trait differences, and  
443 phenotypically plastic responses (Loreau et al., 2010; Cardinale et al., 2012; Sapijanskas  
444 et al., 2014).

445 In line with all these trends, empirical studies are unveiling a key role for top predators,  
446 mega-herbivores and disturbance regimes (fire or other abrupt events) in mediating  
447 links between biodiversity and ecosystem function. For example, the loss of top  
448 predators and/or megaherbivores (and the associated trophic cascades) influence the  
449 dynamics of wildfire, carbon sequestration, invasive species, biogeochemical cycles and  
450 diseases (Schindler et al., 1997; Gill et al., 2009; Smith et al., 2010; Lavery et al., 2010;  
451 Pershing et al., 2010; Estes et al., 2011; Rule et al., 2012; Wolf et al., 2013; Doughty et

452 al., 2013). For example, interactions between top predators, diseases, herbivory, plant  
453 communities, and fire produce large-scale changes in the structure of vegetation and  
454 associated communities (McLaren and Peterson, 1994; Crooks and Soulé, 1999;  
455 Sinclair et al., 2003; Croll et al., 2005; Holdo et al., 2009; Estes et al., 2011; Leganeux  
456 et al., 2014). Similarly, the absence of natural predators, loss of native predators and  
457 reduced top-down control facilitates the performance of invasive species (Estes et al.,  
458 2011). Of note, current biodiversity loss is characterized by the extinction of  
459 megaherbivores and top consumers and larger-bodied animals in general (Estes et al.,  
460 2011).

461         Increased C-N-P imbalances can substantially alter ecosystem functions and  
462 their relationships with biodiversity. For example, the C sequestration and C storage  
463 capacity of terrestrial and aquatic ecosystems depends on changes in the C-N-P  
464 stoichiometric ratios of the system components, the total supply of nutrients from  
465 external sources, and the relative distribution of C-N-P elements between system  
466 components (Hessen et al., 2004; Peñuelas et al., 2013a). On the other hand, changes in  
467 food web structure, and in the composition of herbivores and predators can also alter  
468 carbon sequestration and promote source-sink shifts (e.g. Schindler et al., 1997; Lavery  
469 et al., 2010; Pershing et al., 2010). In oceans, the sequestration of CO<sub>2</sub> occurs due to the  
470 under-saturation water pCO<sub>2</sub> with respect to the atmosphere (the “Solubility pump”) and  
471 subsequent transport to depth waters (Hessen et al., 2004; Barton et al., 2013).

472 Deposition of N and other macronutrients from the atmosphere may have important  
473 effects on the biological pump over long time scales. Changes in C/nutrient ratios of  
474 export organic matter and in nitrogen-fixing and denitrification processes can  
475 significantly alter C sequestration in oceans (Hessen et al., 2004; Barton et al., 2013).

476 Moreover, biodiversity loss of top herbivores (e.g. whales) may significantly alter

477 nutrient recycling processes, biotic pump processes and carbon uptake (Roman and  
478 McCarthy, 2010; Lavery et al., 2010; Pershing et al., 2010). At much larger temporal  
479 scales, positive feedbacks and compensatory negative feedbacks link ocean productivity,  
480 phosphorus availability, anoxia and the suppression of Organic matter-P and Fe-P burial  
481 (Handoh and Lenton, 2003). Million-year periodic changes in ocean N-P nutrient  
482 availability have been associated with major shifts on Earth biodiversity (Handoh and  
483 Lenton, 2003). In terrestrial systems, changes in litter C/N and C/P ratios determine  
484 nutrient release and immobilization, and decomposer carbon-use efficiency. Higher  
485 nitrogen and phosphorus concentrations are usually associated with more rapid  
486 decomposition rates (Manzoni et al., 2008, 2010). In addition, biodiversity loss and  
487 changes in the structure food webs can significantly influence decomposition processes  
488 and alter litter C-N-P ratios (Frank and Groffman, 1998; Mulder and Elser, 2009;  
489 Cardinale et al., 2012).

490 Overall, all this empirical evidence suggests that human-induced global C-N-P  
491 imbalances may produce multiple interactions and feedbacks between biodiversity and  
492 basic ecosystem functions. During the next decades, ecosystem functions will  
493 simultaneously respond to increased C-N-P imbalances and global warming, changes in  
494 the geographic distribution of functional groups, invasive species, the loss of top  
495 predators and mega-bervivores, altered disturbance regimes and habitat destruction and  
496 alteration, among other drivers (Peñuelas and Carnicer 2010, Carnicer and Peñuelas  
497 2012, Peñuelas et al., 2013b). Moreover, recent assesments suggest that the impacts of  
498 biodiversity loss on ecosystem function are of comparable magnitude to the impacts of  
499 drought, climate warming, ozone, acidification, elevated CO<sub>2</sub>, herbivory, fire and  
500 pollution (Tilman et al., 2012; Hooper et al., 2012).

501

502 **Acknowledgements:** This research was supported by VENI-NWO 863.11.021 and the  
503 Spanish Government projects CGC2010-17172 and Consolider Ingenio Montes  
504 (CSD2008-00040) and by the Catalan Government project SGR 2009-458.

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1220 **Table 1.** A non-exhaustive summary of the different hypotheses associated with large-  
 1221 scale gradients in species' stoichiometry.  
 1222

Hypothesis	Description	References
Optimality, fitness maximisation and trade-offs between diverse life history, functional, stoichiometric and biochemical traits.	Fitness maximisation, trade-offs and the operation of natural selection drives the evolution of stoichiometric traits. The evolution of metabolic networks is constrained by elementary mass balance and thermodynamic laws	Parker and Maynard Smith, 1990; Klausmeier et al., 2004; Orth et al., 2010; Loladze and Elser, 2011; Daines et al., 2014
Growth rate hypothesis	Differences in organism C-N-P stoichiometry reflect increased allocation to P-rich ribosomal RNA at higher growth rates	Elser et al. 1996; Sterner and Elser, 2002; Loladze and Elser, 2011
Substrate age hypothesis	Tropical soils are often older, more leached, and have lower fertility, which can lead to reduced organism N and P with increased temperature across geographic gradients	Walker and Syers, 1976; Reich and Oleksyn, 2004
Temperature–plant physiology hypothesis	Plants grown at low temperatures develop greater leaf N and P content, to offset reduced rates of biochemical reactions caused by the diminished efficiency of N-rich enzymes and P-rich RNA	Woods et al., 2003; Reich and Oleksyn, 2004
Endothermy	Nutritional requirements of endotherms and ectotherms deviate largely and significantly affect whole organism stoichiometry	Klaassen and Nolet, 2008; Wilkinson and Ruxton, 2013
Temperature–biogeochemistry hypothesis	Low temperatures depress decomposition and mineralization of organic matter, reduce the availability of N and P, and significantly alter the stoichiometry of species	Reich and Oleksyn, 2004
Trophic position, Herbivory	Trophic position is associated with significant changes	Elser et al., 1996;

	in C-N-P stoichiometry. Heterotrophs are often less rich in C than autotrophs and need to excrete/egest excess C, and this may come at a considerable metabolic cost	Fagan et al., 2002; Urabe et al., 2002; Hall et al., 2007; Daines et al., 2014
Taxonomic composition, evolutionary constraints and niche conservatism	Systematic differences in macronutrient composition (C-N-P) are phylogenetically conserved	Quigg et al., 2003; Woods et al., 2003, 2004
Regional differences in the species composition	Regional differences in the species composition of the plankton community drive the N/P ratio of biological nutrient removal across geographic gradients	Weber and Deutsch, 2010
Body mass and allometry	RNA tissue content, structural tissues and organism N/P ratios show allometric relationships that are determined by species-specific evolutionary processes and the emergence of contrasting life history strategies.	Peters, 1983; Elser, 1996; Sterner and Elser, 2002; Mulder and Elser, 2009
Ontogenetic stage	Ontogenetic changes are associated with changes in biochemical and cellular composition and other allocation decisions, producing changes in body N/P ratio and C-N-P stoichiometry.	Elser et al., 1996; Sterner and Elser, 2002
Structural material and differential allocation on tissues	Tissues significantly differ in nutrient composition. Inter- and intra-specific differences in allocation and tissue structures motivate significant changes in body C-N-P stoichiometry	Elser et al., 1996; Vanni et al., 2002
Differential investments in basic life-history functions (reproduction, storage, defense)	Differential investments in basic life-history functions (reproduction, storage, defense) alter body stoichiometry	Ventura and Catalan, 2005; Tao et al., 2010.
Active regulation of nutrient uptake, excretion, N <sub>2</sub> fixation, reabsorption	Diverse physiological processes actively regulate body nutrient content and determine stoichiometry	Sterner and Elser, 2002; Sardans et al., 2012ab; Sardans and Peñuelas. 2012
Species-specific P and N storage strategies	Species develop evolutionary strategies and adaptations to store limiting resources, affecting in turn body stoichiometry	Martin and van Mooy, 2012; Daines et al., 2014

Resource supply stoichiometry	Resource supply stoichiometry affects the stoichiometric composition of consumers through diverse metabolic and ecophysiological processes, phenotypically plastic responses and long-term adaptive responses	Elser et al., 1996; Sturner et al., 1997; 1998; Hillebrand and Kahlert, 2001; Sturner and Elser, 2002; Woods et al., 2002; Schade et al., 2003; Klausmeier et al., 2004; Elser et al., 2006; Acquisti et al., 2009; Small and Pringle, 2010; Frost et al., 2010.
Genome and cell size	Genome and cell size affect multiple traits and the elemental composition of whole cells and organisms	Hessen et al., 2010; Kozłowski et al., 2003
Stoichiometric plasticity and stoichiometric homeostasis	Phenotypically plastic responses and regulatory physiological and biochemical processes can modify organism C-N-P stoichiometry	Hessen et al., 2004; Persson et al., 2010
Spatiotemporal gradients in conditions and resources (light, nutrients, rainfall, Fe, Si, other conditions and resources)	The spatiotemporal variation of conditions and resources significantly influences organism stoichiometry	Urabe and Sturner, 1996; Sturner et al., 1997, 1998; Klausmeier et al., 2004; Diehl 2007; Martiny et al., 2013; Barton et al., 2013
Topographic gradients associated with changes in N deposition, gradients in temperature and rainfall and other factors	Topography correlates with the clinal variation of environmental conditions, resources and ecological processes that induce changes in organism stoichiometry	Bobbink et al., 2010
Environmental filtering	The demographic performance and local persistence of populations depend on trait-environment interactions. These interactions filter some species and can influence the observed stoichiometric patterns at the species or	Carnicer et al., 2008; Carnicer et al., 2012; Daines et al., 2014

	community level.	
Long-term periodic variations in nutrient cycling dynamics	Long-term periodic variations in nutrient cycling dynamics at geological time-scales alter Earth diversity, and the evolution of species' stoichiometry.	Tyrrell 1999; Lenton and Watson, 2000; Handoh and Lenton, 2003; Lenton and Klausmeier, 2007
Biogeochemical niche	Pant species occupy different biogeochemical niches, and differ significantly in key physiological, structural and stoichiometric traits	Peñuelas et al., 2008, 2010
Species richness	Species richness and functional groups richness affect community stoichiometry, and alter C/P and N/P ratios. Community composition affects the biochemical niche of species across functional groups	Abbas et al. 2013; Urbina et al., 2014

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1239 **Table 2.** Summary of the PCA analysis for species-specific traits (number of host-  
1240 plants, dispersal capacity and flight period length) and habitat variables (habitat aridity  
1241 breadth, habitat winter temperature breadth) for 169 Butterflies in Catalonia, Spain. A  
1242 major axis of life history variation was observed, ranging from multivoltine trophic  
1243 generalists with high dispersal capacity to univoltine (i.e. one generation per year),  
1244 trophic specialist species with low dispersal capacity (see supplementary methods for  
1245 further details). The values for the factors (habitat aridity breadth, habitat winter  
1246 temperature breadth, number of host-plants, dispersal capacity, flight period length) are  
1247 the loadings on PCA axis 1.

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	<b>PCA 1</b>
Eigenvalue	2.97
Explained variance	59.49
Habitat aridity breadth	0.50
Habitat winter temperature breadth	0.48
Number of host-plants	0.37
Dispersal capacity	0.42
Flight-period length	0.45

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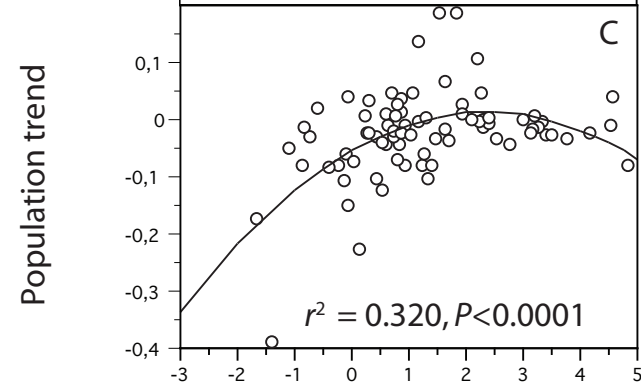
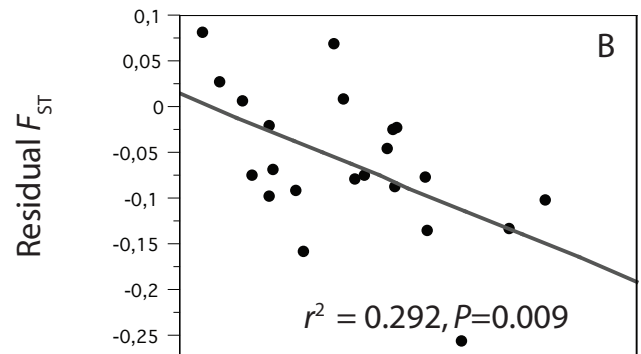
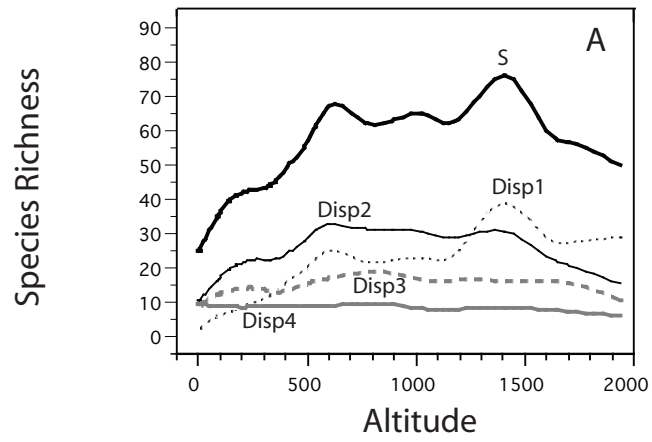
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1259 **Figure 1.** The adaptive trait continuum in Mediterranean butterflies. This functional  
1260 trait continuum is described by the scores along the PCA axis 1 of 169 butterfly species  
1261 (see Table 2, Carnicer et al 2013a and supplementary methods for further details). A)  
1262 Observed distribution of major functional groups along an altitudinal gradient (modified  
1263 from Stefanescu et al 2011). S: total butterfly species richness, Disp4: species richness  
1264 of highly dispersive species; Disp3: species richness of high-medium dispersive species;  
1265 Disp2: species richness of medium-low dispersive species; Disp1: species richness of  
1266 low dispersive species. B) Observed relationship of the adaptive trait continuum (PCA)  
1267 with genetic variability ( $F_{ST}$ ). C) Observed relationship of the adaptive trait continuum  
1268 (PCA) with regional population trends. Population trends were estimated as the slope of  
1269 log-linear regression of abundances from the period 1994-2008 using TRIM software  
1270 and were available for 78 species.



Butterfly functional trait continuum (PCA)

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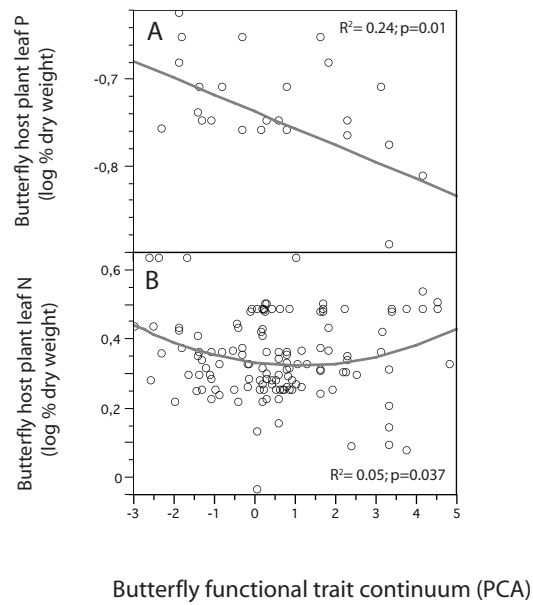
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1275 **Figure 2.** Observed relationships between the adaptive trait continuum of  
1276 Mediterranean butterflies (PCA) and A) leaf P content; B) Leaf N content of the host  
1277 plants. See supplementary methods for further details.



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1290 **Supplementary methods** for Figures 1, 2 and 3 (modified from Carnicer et al. 2012)  
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1293 The Catalan Butterfly Monitoring Scheme (CBMS; [www.catalanbms.org/](http://www.catalanbms.org/)) and the  
1294 Andorran Butterfly Monitoring Scheme (BMSAnd; [www.bmsand.ad/](http://www.bmsand.ad/)) consist of a  
1295 network of recording sites in the northeast of the Iberian Peninsula that are monitored  
1296 on a weekly basis from March to September (30 sampling weeks per year) by means of  
1297 visual counts along fixed routes (for further details, see Stefanescu, Carnicer and  
1298 Peñuelas, 2011a). For Figs. 1,2 and 3, we used data from 84 transect routes (mean  
1299 length = 1785 m; S.D. = 821 m; range: 565-4909 m) monitored between 1994 and 2007.  
1300 A total of 169 butterfly species was recorded and considered in the analyses.  
1301 For each sampling transect, we extracted from the Digital Climatic Atlas of Catalonia  
1302 ([http://www.opengis.uab.cat/acdc/english/en\\_model.htm](http://www.opengis.uab.cat/acdc/english/en_model.htm)) the mean winter temperature  
1303 (January data), the mean annual temperature and the mean annual rainfall, and derived  
1304 an aridity index (the modified Gaussen aridity index; see Stefanescu et al., 2011a). For  
1305 each butterfly species, we recorded the number of transect routes on which it was  
1306 detected (distribution range). Following Swanson and Garland (2009), we estimated the  
1307 mean temperature along the transect routes where a species was found (habitat mean  
1308 temperature) and calculated the range in degrees Celsius between the maximum and  
1309 minimum habitat mean temperature values reported (habitat winter temperature breath).  
1310 These calculations were carried out for mean winter temperature, mean annual  
1311 temperature and the Gaussen aridity index. The duration of the flight period in

1312 Catalonia (number of months with flight activity) for each species ('flight period  
1313 length') was obtained from independent observations in the study area with precise  
1314 sampling dates. In addition, species were classified according to the trophic  
1315 specialization of their larvae. We also recorded the number of host-plant families,  
1316 genera and species used by each butterfly species. Species were also classified  
1317 according to their dispersal capacity (following Stefanescu et al., 2011a). Each butterfly  
1318 species was assigned an index of increasing mobility ('dispersal capacity') ranging from  
1319 1 to 4, according to the following criteria: 1, species living in metapopulations with very  
1320 little dispersal between populations; 2, species living in metapopulations with a lot of  
1321 dispersal between populations; 3, species living in patchy populations with non-  
1322 seasonal migration; 4, species living in patchy populations with seasonal migration.  
1323 Data on dispersal capacity and population structure were extracted from Pollard and  
1324 Eversham (1995), Dennis and Shreeve (1996), and adapted from personal observations  
1325 in the study region (Stefanescu et al., 2011a). For Fig. 3, plant trait data (leaf N, P [log  
1326 % dry weight]) was obtained from Wright et al., (2004). See Carnicer et al., 2012,  
1327 2013a for further methodological details.

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