

1           Reevaluating Europe's other debt with improved statistical tools

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17 Abstract:

18 Dullinger et al. (PNAS, 2013) showed that current proportions of threatened species in  
19 European countries are more correlated to socio-economic pressures calculated a  
20 century ago than to current socio-economic pressures. These results could have  
21 important impacts on future political decisions, yet the statistical analyses used may be  
22 strongly impacted by pseudo-replication and over-dispersion of data.

23 I reanalysed Dullinger et al.'s data using generalised linear mixed models accounting  
24 for pseudo-replication and over-dispersion.

25 These new statistical models indicated that socio-economic pressures had a much less  
26 clear impact on proportions of threatened species than indicated by Dullinger et al. In  
27 many cases, the effects of socio-economic pressures even vanished.

28 Dullinger et al. (2013)'s results are actually much less "considerable" than their paper  
29 implies and therefore should be viewed with caution. Ecologists should more often  
30 incorporate pseudo-replication and overdispersion in their statistical analyses.

31

32 Keywords: pseudo-replication; overdispersion; binomial distribution; statistical model;  
33 generalized linear mixed models; biodiversity; indicator; threatened species; socio-economic  
34 pressures

35

36 **Introduction**

37 Dullinger et al. (2013) showed that current proportions of threatened species in 22 European  
38 countries respond more to socio-economic pressures calculated a century ago than to current  
39 socio-economic pressures. Based on generalised linear mixed models (GLMMs), the authors  
40 found very clear discrepancies among the statistical models involving socio-economic  
41 pressures in 1900, 1950 and 2000 – with the 1900 model being the best. They also found  
42 fixed-effect estimators that were very significantly different from 0 for all three models (cf.  
43 their Table 1). They concluded that “irrespective of recent conservation actions, large-scale  
44 risks to biodiversity lag considerably behind contemporary levels of socioeconomic  
45 pressures”.

46 These results could have important impacts on future political decisions, yet I have serious  
47 doubts about the way Dullinger et al. analysed their data. To be brief, they completely  
48 overlooked the possible influence of pseudoreplication and overdispersion. Regarding  
49 pseudo-replication, although the same socioeconomic variables were repeatedly applied to the  
50 seven taxonomic groups in each country, the statistical models did not include a random effect  
51 for country. This means that the data was analysed as if the socio-economic variables came  
52 from completely different countries. Concerning over-dispersion, after having taken into  
53 account the effect of socio-economic pressures and variations in the intercept among taxa, the  
54 proportion of threatened species might not be distributed like a classical binomial distribution  
55 but instead, may be over-dispersed compared to the binomial distribution. This is simply  
56 because substantial variations in the ratio of threat among countries – for single taxon  
57 analyses – or among taxa within countries – for multi-taxa analyses – might still remain even  
58 after having modeled these effects. Not taking into account pseudo-replication and

59 overdispersion in the model is known to have deleterious effects on the standard errors of the  
60 estimates (Millar and Anderson 2004; Warton and Hui 2011), and thus on statistical tests. It  
61 also has some impact on the model comparison criteria.

## 62 **Material and methods**

63 Using the data published as supplementary material by Dullinger et al. (2013) complemented  
64 by data on the number of extinct species kindly supplied by S. Dullinger, I refitted the  
65 binomial GLMMs used by Dullinger et al. to analyze the link between the proportion of  
66 threatened species and the three socio-economic pressures – human population density, per  
67 capita GDP and human appropriation of net primary productivity –, quantified either in 1900,  
68 1950 or 2000, and synthesized by a principal component analysis. I used R3.1.1 and the R  
69 libraries lme4 and AICcmodavg to fit and analyse both the multi-taxa and single taxon  
70 models. This was done in connection with S. Dullinger. While working with the  
71 Supplementary data, we realized that there was a mistake in the published version: the human  
72 appropriation of net primary productivity for Romania in 1900 was 0.279 and not 0.297. At  
73 the multi-taxa level, I first refitted Dullinger et al.'s models – except that I included  
74 grasshoppers, which Dullinger et al. had not done due to a coding error (Dullinger, personal  
75 communication). To allow for overdispersion and take pseudo-replication into account, I then  
76 fitted a new model by adding a random Country effect to the intercept and included a  
77 normally distributed random intercept (e.g. Warton and Hui 2011). At the single-taxon level, I  
78 similarly refitted Dullinger et al.'s models and also created new models incorporating a  
79 random Country effect to allow for over-dispersion. In addition, in both cases, I fitted a null  
80 model, with no fixed effect other than the intercept, to not only compare the socio-economic  
81 models among themselves but also with a model with no such effect. I interpreted the models  
82 using some of Dullinger et al.'s methods, by presenting the estimators and their confidence

83 intervals of the fixed effects (as well as of the standard deviations of the random effects), the  
84 corrected Akaike Information Criterion (AICc) and the associated model weights (AW) for the  
85 four multi-taxa models and a graphical representation of the Akaike weights of the four  
86 models for each of the single-taxon model. AICc was calculated based on the degrees of  
87 freedom as estimated from the lmer object, as did Dullinger et al. This involves what a  
88 Bayesian would call hyperparameters, i.e. fixed effects and variance parameters. I  
89 acknowledge that this choice has not yet been stabilized for mixed models (e.g. Spiegelhalter  
90 et al. 2002). I therefore also report the log-likelihood of each model to allow the reader to  
91 compute other model selection criteria.

92

### 93 **Results**

94 The standard deviation of the added random effects in the multi-taxa models turned out to be  
95 between 0.34 and 0.53. These added levels of variation had a considerable effect on the results  
96 (cf. Table 2), which proved to be much less clearcut than those given by Dullinger et al. (cf.  
97 Table 1). Even if the best model remained the one with the 1900 socio-economic indicators,  
98 the Akaike weights were much more evenly spread among models and the Akaike weight of  
99 the null model (0.26) was non negligible. Also, fewer estimators were significantly different  
100 from zero.

101 For the single-taxon models, there was a systematic shift between Dullinger et al.'s best  
102 model, which included one set of socio-economic indicators, and the best model when  
103 over-dispersion was incorporated, which included no socio-economic indicators (Figure 1).

104

### 105 **Discussion**

106 Some readers might mainly view the new multi-taxa results as being qualitatively the same as  
107 in the original publication. This line of interpretation would be acceptable if the main message

108 to scientists and to decision makers in our scientific studies were merely qualitative. However,  
109 such an attitude could relegate science to the story telling realm. Quantitative aspects are also  
110 very important. Granted, with the original analyses, we have no doubt about which model is  
111 the best of the four fitted models, nor do we doubt the significance of the effects in these  
112 models. Yet, as I explained in the introduction, these analyses are not correct. There is other  
113 evidence to indicate that the original models have quantitative problems. Firstly, when we  
114 simulate data with levels of over-dispersion and pseudo-replication as estimated with the new  
115 methods and with no effect of the socio-economic pressures, and when we analyse these data  
116 with Dullinger et al.'s methods, we get results that are very much in line with those we  
117 obtained in Table 1 in terms of significance of the effects and of the distribution of Akaike  
118 weights. Another clue indicating there are some statistical problems with the original models  
119 is that the error in the data for net primary productivity for Romania in 1900 indicated in the  
120 material and methods section (0.297 instead of 0.279) – which is a rather minor error with  
121 respect to the range of variation for this variable – yielded an AICc shift of more than 30 units  
122 – a huge difference!

123 The new statistical analyses, taking into account both pseudo-replication and over-dispersion  
124 indicated that the results are much less clear cut, leaving greater room for doubt as to which  
125 one is the best model. This doubt increases further when we consider the single-taxon  
126 analyses, all of which indicated that the best model of the four was the one without any  
127 socio-economic indicator.

128 I therefore conclude from the re-analyses of Dullinger et al's data that their results are actually  
129 much less “considerable” than their paper implies and should be viewed with caution. I would  
130 also like to remind ecologists of a classical warning (Hurlbert 1984; White and Bennetts  
131 1996; Millar and Anderson 2004; Noe et al. 2010; O'Hara and Kotze 2010; Warton and Hui  
132 2011): great care should be taken to incorporate sources of variation corresponding to

133 pseudo-replication and over-dispersion into statistical analyses of count data.

134

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141 **References:**

142 Dullinger S, Essl F, Rabitsch W, Erb KH, Gingrich S, Haberl H, Hülber K, Jarošík V,  
143 Krausmann F, Kuřn I, Pergl J, Pyšek P, Hulme PE (2013) Europe's other debt crisis caused by  
144 the long legacy of future extinctions. *Proc Nat Acad Sciences USA* 110:7342-7347. doi:  
145 10.1073/pnas.1216303110

146 Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecol*  
147 *Monogr* 54:187-211.

148 Millar RB, Anderson MJ (2004) Remedies for pseudoreplication. *Fish Research* 70:397-407.  
149 doi: 10.1016/j.fishres.2004.08.016

150 Noe DA, Bailer AJ, Noble RB (2010) Comparing methods for analyzing overdispersed count  
151 data in aquatic toxicology. *Envir Toxicol Chemis* 29:212-219. doi: 10.1002/etc.2

152 O'Hara RB, Kotze DJ (2010) Do not log-transform count data. *Meth Ecol Evol* 1:118-122.  
153 doi: 10.1111/j.2041-210X.2010.00021.x

- 154 Spiegelhalter DJ, Best NG, Carlin JB, van der Linde A (2002) Bayesian measures of model  
155 complexity and fit (with Discussion). *J Roy Statist Soc B*, 64:583-616. doi:  
156 10.1111/1467-9868.00353
- 157 Warton DI, Hui F (2011) The arcsine is asinine: the analysis of proportions in ecology.  
158 *Ecology* 92:3-10. doi: 10.1890/10-0340.1
- 159 White GC, Bennetts RE (1996) Analysis of frequency count data using the negative binomial  
160 distribution. *Ecology* 77:2549-2557.



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162 Table 1. Results of Dullinger et al. (2013)'s statistical models, not accounting for  
 163 pseudo-replication among countries and over-dispersion, of proportions of threatened species  
 164 from seven taxonomic groups and 22 European countries as explained –or not – by  
 165 socioeconomic indicators calculated at different dates.

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	Null model	1900 model	1950 model	2000 model
Estimate for PC1	-	0.206 ([0.193;0.218]) ****	0.159 ([0.146;0.174]) ****	0.110 ([0.095;0.122]) ****
Estimate for PC2	-	0.139 ([0.116;0.163]) ****	0.040 ([0.022;0.059]) ***	-0.058 ([-0.075;-0.040]) ***
Estimate for PC3	-	-0.346 ([-0.381;-0.311]) ****	0.181 ([0.143;0.219]) ****	0.124 ([0.075;0.173]) ***
Standard deviation of Taxon random effect	0.276 ([0.095;0.404])	0.306 ([0.113;0.429])	0.284 ([0.113;0.399])	0.280 ([0.104;0.422])
Log-likelihood	-3463.9	-2770.5	-3173.9	-3328.4
AICc	6931.8	5551.4	6358.3	6667.3
AW	<10 <sup>-9</sup>	1	<10 <sup>-9</sup>	<10 <sup>-9</sup>

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168 Fixed effects (omitting the intercept), standard deviation of random effects, log-likelihood,  
169 corrected Akaike information criterion (AICc), and Akaike weights (AW) for binomial  
170 generalized mixed-effects models not allowing for pseudoreplication among countries and  
171 overdispersion relating the variation in the proportion of red-listed species to either no effect  
172 or historical (1900 and 1950) or contemporary (2000) values of socioeconomic indicators.  
173 These indicators – human population density, per capita GDP and human appropriation of net  
174 primary productivity – were subjected to a principal component analysis before fitting the  
175 regression models, yielding three uncorrelated variables (PC1, PC2 and PC3). Estimates  
176 include the mean estimate, the 95% confidence interval estimated with the standard bootstrap  
177 method (confint function in library lme4) in parentheses and the level of significance of  
178 difference from 0 at the end (\* for  $P < 0.05$ , \*\* for  $P < 0.01$ , \*\*\* for  $P < 0.001$  and \*\*\*\* for  
179  $P < 10^{-9}$ ). AICc and AW were calculated with the aictable function in the AICcmodavg R  
180 library. The results are slightly different from those in Table 1 in Dullinger *et al.* (2013)  
181 because the analyses here include the data for grasshoppers, which were left out of the  
182 analyses published in Dullinger *et al.* (2013) (S. Dullinger, personal communication).

183

184

185 Table 2. Results of statistical models accounting for pseudo-replication among countries and  
 186 over-dispersion, of proportions of threatened species from seven taxonomic groups and 22  
 187 European countries as explained –or not – by socioeconomic indicators calculated at  
 188 different dates, in.

	Null model	1900 model	1950 model	2000 model
Estimate for PC1	-	0.209 ([0.086;0.327]) **	0.187 ([0.042;0.335]) **	0.169 ([0.029;0.308]) *
Estimate for PC2	-	-0.007 ([-0.242;0.243])	-0.054 ([-0.279;0.155])	-0.064 ([-0.261;0.150])
Estimate for PC3	-	0.116 ([-0.196;0.456])	-0.208 ([-0.608;0.169])	-0.222 ([-0.710;0.297])
Standard deviation of Taxon random effect	0.342 ([0.000;0.468])	0.306 ([0.000;0.472])	0.303 ([0.000;0.446])	0.302 ([0.000;0.465])
Standard deviation of Country random effect	0.460 ([0.274;0.617])	0.346 ([0.021;0.469])	0.368 ([0.090;0.465])	0.386 ([0.074;0.494])
Standard deviation of Country*Taxon random effect	0.525 ([0.427;0.633])	0.527 ([0.423;0.630])	0.529 ([0.421;0.627])	0.529 ([0.431;0.624])
Log-likelihood	-554.9	-550.4	-551.3	-552.0
AICc	1118.1	1115.6	1119.0	1117.5

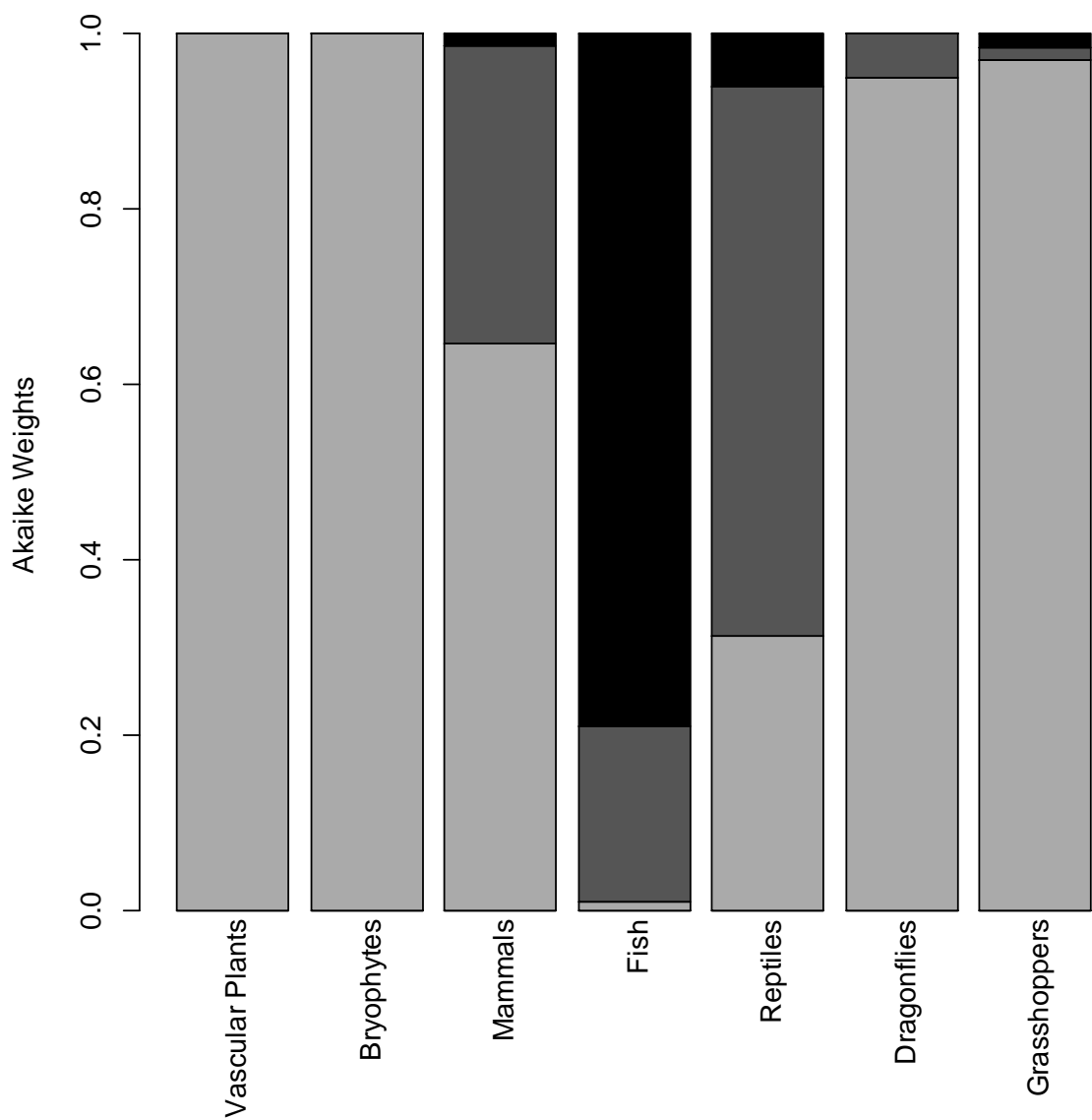
AW	0.156	0.536	0.207	0.101
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190 Fixed effects (omitting the intercept), standard deviations of random effects, log-likelihood,  
191 corrected Akaike information criterion (AICc), and Akaike weights (AW) for binomial  
192 generalized mixed-effects models allowing for pseudo-replication and over-dispersion relating  
193 the variation in the proportion of red-listed species to either no effect or historical (1900 and  
194 1950) or contemporary (2000) values of socioeconomic indicators. Notations and methods are  
195 as in Table 1. AICc values should be compared only among models in Table 2, not with  
196 models from Table 1 which have different types of random effects. Akaike Weights were  
197 much more evenly spread among models and fixed effects were much less significant than in  
198 Table 1.

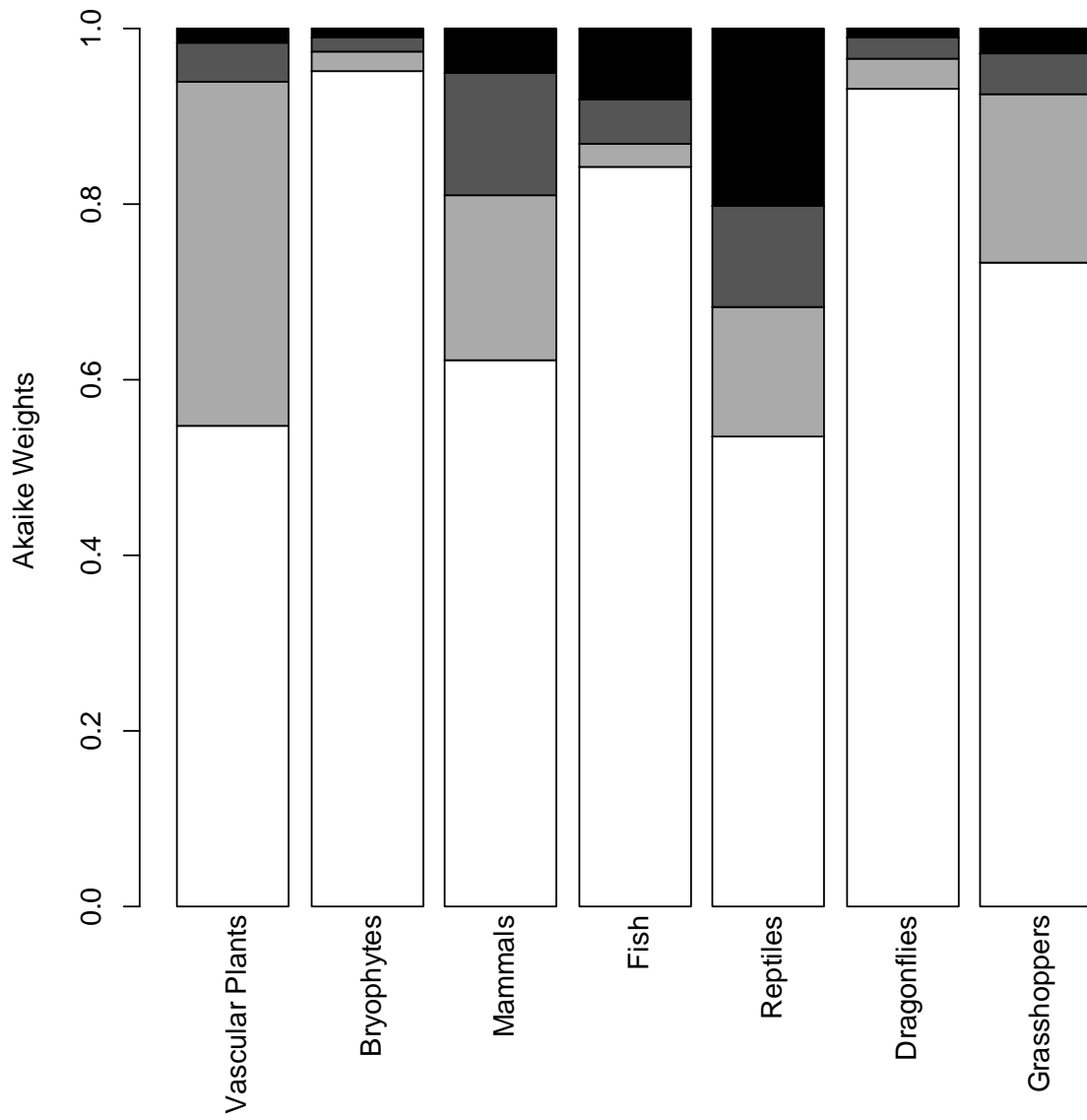
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207 Figure 1. Relative support (Akaike Weights) for models explaining the proportion of  
208 red-listed species in each of the seven taxonomic groups in 22 European countries. The  
209 models incorporated either only an intercept (white color), or historical (1900, light gray;  
210 1950, dark gray) or contemporary (2000, black) levels of socio-economic impact indicators  
211 (human population density, per capita GDP, human appropriation of net primary productivity).  
212 (a) Statistical models that did not model overdispersion, as in Dullinger et al. (2013); (b)  
213 Statistical models including over-dispersion.

214