



**HAL**  
open science

## Directional trends in species composition over time can lead to a widespread overemphasis of year-to-year asynchrony

Enrique Valencia, Francesco de Bello, Jan Lepš, Thomas Galland, Anna E-vojtíkó, Luisa Conti, Jiří Danihelka, Jürgen Dengler, David Eldridge, Marc Estiarte, et al.

### ► To cite this version:

Enrique Valencia, Francesco de Bello, Jan Lepš, Thomas Galland, Anna E-vojtíkó, et al.. Directional trends in species composition over time can lead to a widespread overemphasis of year-to-year asynchrony. *Journal of Vegetation Science*, 2020, 31 (5), pp.792-802. 10.1111/jvs.12916 . hal-03033474

**HAL Id: hal-03033474**

**<https://hal.science/hal-03033474>**

Submitted on 26 Dec 2020

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Directional trends in species composition over time can lead to a widespread**  
2 **overemphasis of year-to-year asynchrony**

3  
4 **Running title: Directional trends effects on synchrony**

5  
6 Enrique Valencia<sup>1\*†</sup>, Francesco de Bello<sup>2,3†</sup>, Jan Lepš<sup>2,4</sup>, Thomas Galland<sup>2,5</sup>, Anna E-  
7 Vojtková<sup>2,5</sup>, Luisa Conti<sup>5,6</sup>, Jiří Danihelka<sup>7,8</sup>, Jürgen Dengler<sup>9,10,11</sup>, David J. Eldridge<sup>12</sup>,  
8 Marc Estiarte<sup>13,14</sup>, Ricardo García-González<sup>15</sup>, Eric Garnier<sup>16</sup>, Daniel Gómez<sup>15</sup>, Susan  
9 Harrison<sup>17</sup>, Tomas Herben<sup>18,19</sup>, Ricardo Ibáñez<sup>20</sup>, Anke Jentsch<sup>21</sup>, Norbert Juergens<sup>22</sup>,  
10 Miklós Kertész<sup>23</sup>, Katja Klumpp<sup>24</sup>, Frédérique Louault<sup>24</sup>, Rob H. Marris<sup>25</sup>, Gábor  
11 Ónodi<sup>23</sup>, Robin J. Pakeman<sup>26</sup>, Meelis Pärtel<sup>27</sup>, Begoña Peco<sup>28</sup>, Josep Peñuelas<sup>13,14</sup>,  
12 Marta Rueda<sup>29</sup>, Wolfgang Schmidt<sup>30</sup>, Ute Schmiedel<sup>22</sup>, Martin Schuetz<sup>31</sup>, Hana  
13 Skalova<sup>8</sup>, Petr Šmilauer<sup>32</sup>, Marie Šmilauerová<sup>2</sup>, Christian Smit<sup>33</sup>, Ming-Hua Song<sup>34</sup>,  
14 Martin Stock<sup>35</sup>, James Val<sup>12</sup>, Vigdis Vandvik<sup>36</sup>, Karsten Wesche<sup>11,37,38</sup>, Ben A.  
15 Woodcock<sup>39</sup>, Truman P. Young<sup>40,41</sup>, Fei-Hai Yu<sup>42</sup>, Martin Zobel<sup>27</sup>, Lars  
16 Götzenberger<sup>2,5</sup>.

17  
18 <sup>1</sup> Departamento de Biología y Geología, Física y Química Inorgánica, Escuela Superior  
19 de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, Móstoles,  
20 Spain.

21 <sup>2</sup> Department of Botany, Faculty of Sciences, University of South Bohemia, České  
22 Budějovice, Czech Republic.

23 <sup>3</sup> Centro de Investigaciones sobre Desertificación (CSIC-UV-GV), Valencia, Spain.

24 <sup>4</sup> Biology Research Centre, Institute of Entomology, Czech Academy of Sciences,  
25 České Budějovice, Czech Republic.

26 <sup>5</sup> Institute of Botany, Czech Academy of Sciences, Třeboň, Czech Republic.

27 <sup>6</sup> Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Praha,  
28 Czech Republic.

29 <sup>7</sup> Department of Botany and Zoology, Masaryk University, Brno, Czech Republic.

30 <sup>8</sup> Institute of Botany, Academy of Sciences of the Czech Republic, Průhonice, Czech  
31 Republic.

32 <sup>9</sup> Vegetation Ecology Group, Institute of Natural Resource Sciences (IUNR), Zurich  
33 University of Applied Sciences (ZHAW), Wädenswil, Switzerland.

34 <sup>10</sup> Plant Ecology Group, Bayreuth Center for Ecology and Environmental Research  
35 (BayCEER), University of Bayreuth, Bayreuth, Germany.

36 <sup>11</sup> German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig,  
37 Leipzig, Germany.

38 <sup>12</sup> Biological, Earth and Environmental Sciences, University of New South Wales,  
39 Sydney, Australia.

40 <sup>13</sup> CREAM, Cerdanyola del Vallès, Catalonia, Spain.

41 <sup>14</sup> CSIC, Global Ecology Unit CREAM-CSIC-UAB, Catalonia, Spain.

42 <sup>15</sup> Instituto Pirenaico de Ecología (IPE-CSIC), Jaca-Zaragoza, Spain.

43 <sup>16</sup> CEFÉ, CNRS, Univ Montpellier, Univ Paul Valéry Montpellier 3, EPHE, IRD,  
44 Montpellier, France.

45 <sup>17</sup> Department of Environmental Science and Policy, University of California Davis,  
46 CA, USA.

47 <sup>18</sup> Department of Botany, Faculty of Science, Charles University, Praha, Czech  
48 Republic.

49 <sup>19</sup> Institute of Botany, Academy of Sciences of the Czech Republic, Průhonice, Czech  
50 Republic.

- 51 <sup>20</sup> Department of Environmental Biology, University of Navarra, Pamplona, Spain.
- 52 <sup>21</sup> Department of Disturbance Ecology, Bayreuth Center of Ecology and Environmental
- 53 Research (BayCEER), University of Bayreuth, Bayreuth, Germany.
- 54 <sup>22</sup> Research Unit Biodiversity, Evolution & Ecology (BEE) of Plants, Institute for Plant
- 55 Science and Microbiology, University of Hamburg, Germany.
- 56 <sup>23</sup> MTA Centre for Ecological Research, Vácrátót, Hungary.
- 57 <sup>24</sup> INRA, VetAgro Sup, UCA, UMR Ecosystem Prairial, Clermont-Ferrand, France.
- 58 <sup>25</sup> University of Liverpool, Liverpool, UK.
- 59 <sup>26</sup> The James Hutton Institute, Craigiebuckler, Aberdeen, UK.
- 60 <sup>27</sup> Department of Botany, Institute of Ecology and Earth Sciences, University of Tartu,
- 61 Tartu, Estonia.
- 62 <sup>28</sup> Terrestrial Ecology Group (TEG), Department of Ecology, Institute for Biodiversity
- 63 and Global Change, Autonomous University of Madrid, Madrid, Spain.
- 64 <sup>29</sup> Department of Conservation Biology, Estación Biológica de Doñana (EBD-CSIC),
- 65 Sevilla, Spain.
- 66 <sup>30</sup> Department of Silviculture and Forest Ecology of the Temperate Zones, University
- 67 of Göttingen, Germany.
- 68 <sup>31</sup> Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Community
- 69 Ecology, Switzerland.
- 70 <sup>32</sup> Department of Ecosystem Biology, Faculty of Science, University of South Bohemia,
- 71 České Budějovice, Czech Republic.
- 72 <sup>33</sup> Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences,
- 73 Groningen, The Netherlands.
- 74 <sup>34</sup> Laboratory of Ecosystem Network Observation and Modelling, Institute of
- 75 Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences,
- 76 Beijing, China.
- 77 <sup>35</sup> Wadden Sea National Park of Schleswig-Holstein, Tönning, Germany.
- 78 <sup>36</sup> Department of Biological Sciences, University of Bergen, Norway.
- 79 <sup>37</sup> Botany Department, Senckenberg, Natural History Museum Goerlitz, Görlitz,
- 80 Germany.
- 81 <sup>38</sup> International Institute Zittau, Technische Universität Dresden, Dresden, Germany.
- 82 <sup>39</sup> NERC Centre for Ecology & Hydrology, Oxfordshire, UK.
- 83 <sup>40</sup> Department of Plant Sciences, University of California, Davis, USA.
- 84 <sup>41</sup> Mpala Research Centre, Nanyuki, Kenya.
- 85 <sup>42</sup> Institute of Wetland Ecology & Clone Ecology / Zhejiang Provincial Key Laboratory
- 86 of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou, China.

87 Correspondence

88 Departamento de Biología y Geología, Física y Química Inorgánica, Escuela Superior

89 de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, Móstoles,

90 Spain.

91 Email: [valencia.gomez.e@gmail.com](mailto:valencia.gomez.e@gmail.com)

92 †Authors contributed equally

93

#### 94 **Funding information**

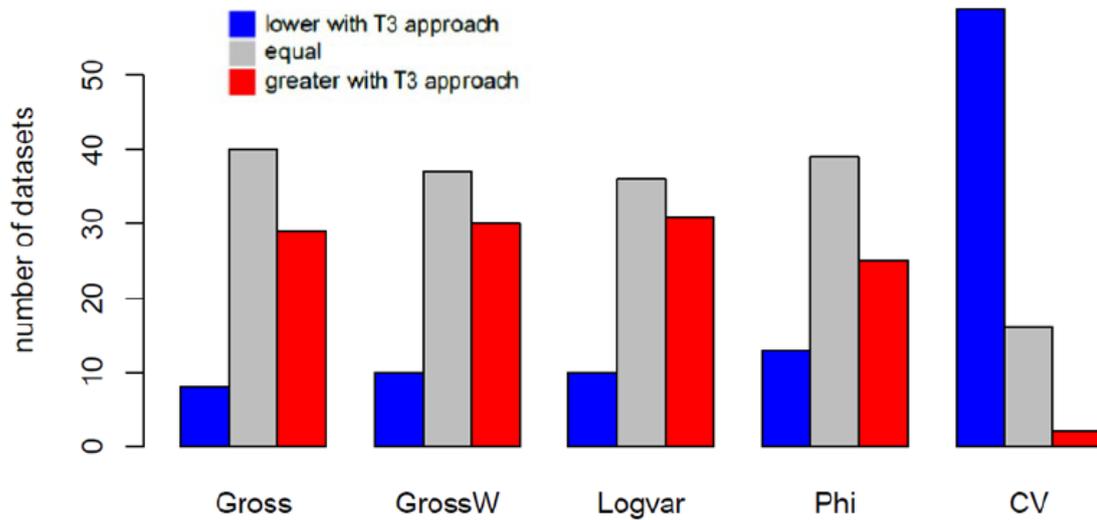
95 Czech Science Foundation (GAČR). Grant Number: 16- 15012S.

96 Program for attracting and retaining talent of Comunidad de Madrid (EV). Grant

97 Number: 2017-T2/AMB-5406

98 **Web summary**

99 Measures of community synchrony and stability aim at quantifying year-to-year  
100 fluctuations in species abundances. However, these indices reflect also long-term  
101 trends, potentially masking year-to-year signals. Using a large number of datasets with  
102 permanent vegetation plots we show a frequent greater synchrony and stability in year-  
103 to-year changes compared to when long-term trends are not taken into account.



104

105 **Abstract**

106 **Questions**

107 Compensatory dynamics are described as one of the main mechanisms that increase  
108 community stability, e.g. where decreases of some species on a year-to-year basis are  
109 offset by an increase in others. Deviations from perfect synchrony between species  
110 (asynchrony) have therefore been advocated as an important mechanism underlying  
111 biodiversity effects on stability. However, it is unclear to what extent existing measures  
112 of synchrony actually capture the signal of year-to-year species fluctuations in the  
113 presence of long-term directional trends in both species abundance and composition  
114 (species directional trends hereafter). Such directional trends may lead to a  
115 misinterpretation of indices commonly used to reflect year-to-year synchrony.

116 **Methods**

117 An approach based on three-term local quadrat variance (T3) which assess population  
118 variability in a three-year moving window, was used to overcome species directional  
119 trend effects. This ‘detrending’ approach was applied to common indices of synchrony  
120 across a Worldwide collection of 77 temporal plant community datasets comprising  
121 almost 7800 individual plots sampled for at least 6 years. Plots included were either  
122 maintained under constant ‘control’ conditions over time or were subjected to different  
123 management or disturbances treatments.

124 **Results**

125 Accounting for directional trends increased the detection of year-to-year synchronous  
126 patterns in all synchrony indices considered. Specifically, synchrony values increased  
127 significantly in ~40% of the datasets with the T3 detrending approach while in ~10%  
128 synchrony decreased. For the 38 studies with both control and manipulated conditions,

129 the increase in synchrony values was stronger for longer-time series, particularly  
130 following experimental manipulation.

### 131 **Conclusions**

132 Species long-term directional trends can affect synchrony and stability measures  
133 potentially masking the ecological mechanism causing year-to-year fluctuations. As  
134 such, previous studies on community stability might have overemphasised the role of  
135 compensatory dynamic in real-world ecosystems, and particularly in manipulative  
136 conditions, when not considering the possible overriding effects of long-term  
137 directional trends.

138

139 **Keywords:** asynchrony, biodiversity, stability, synchrony, temporal dynamics, year-to-  
140 year fluctuation.

141 **Introduction**

142 Given the challenges posed by rapidly changing environments in the context of global  
143 change, it is crucial to understand how biological diversity is maintained over time  
144 (Cardinale et al. 2007; Tomimatsu et al. 2013; Tilman, Isbell, & Cowles 2014). There  
145 is a general consensus toward the role that synchrony (or lack of) in, e.g., year-to-year  
146 population fluctuations between co-existing species plays on species diversity and  
147 community stability (Hautier et al. 2014; Craven et al. 2018). On the one hand, a  
148 common response to environmental fluctuations (for example changes in temperature  
149 or precipitation from one year to another) of most species (synchrony) will tend to  
150 destabilize the community biomass or abundance. On the other hand, the opposite  
151 pattern (compensatory dynamics, i.e. increases or decreases in the relative abundance  
152 of some species that are offset by changes in the relative abundance of others; Hubbell  
153 2001; Gonzalez & Loreau 2009) will lead to higher community stability. In this sense  
154 asynchrony, i.e. the extent of the deviation from lack of perfect synchrony between  
155 species, has been advocated as an important and widespread mechanism that  
156 contributes to stability (Loreau & de Mazancourt 2013).

157 While there is a lively debate on the importance of compensatory dynamics on  
158 the stability of communities (Houlahan et al. 2007; Blüthgen et al. 2016; Lepš et al.  
159 2018) there are also important methodological aspects that can influence the detection  
160 of the underlying biological patterns. Recently, Lepš et al. (2019) demonstrated that the  
161 study of synchrony between species has traditionally disregarded the possible effects of  
162 long-term directional compositional trends in the analysed communities (i.e. a tendency  
163 of some species to increase or decrease over time, or to fluctuate cyclically, Wu et al.  
164 2007). Species directional trends occur when the abundances of species respond not  
165 only to short-term environmental fluctuations, but also to the presence of monotonic or

166 cyclical tendencies over the whole time series considered. Short term environmental  
167 fluctuations (Rabotnov 1974), for example on a year-to-year basis, are expected to  
168 affect species abundance but also to be largely reversible, so that species would not  
169 show long-term directional trends in their abundances. In contrast, long-term  
170 environmental changes, such as climate change, nutrient deposition and changes in land  
171 use (e.g. abandonment or intensification of agricultural land), generally cause long-  
172 term species directional trends (Stevens et al. 2011; Walter et al. 2018). Long-term  
173 directional trends can also be the result of the impact of undetermined drivers  
174 (Milchunas, Lauenroth, & Burkeal 1998). As repeatedly reported by many authors, long  
175 term trends in species abundance are probably omnipresent, and have been  
176 demonstrated even in, now, more than 160 years of the Park Grass Experiment  
177 (Silvertown et al. 2006).

178         To gain a better understanding of the underlying mechanisms regulating  
179 changes in species abundance, short-term fluctuations and long-term trends effects on  
180 synchrony should be disentangled. Unfortunately, this differentiation has been rare in  
181 studies assessing drivers of synchrony and stability (but see Vasseur & Gaedke 2007;  
182 Tredennick et al. 2017; and the review by Lepš et al. 2019). Indeed, using simulations  
183 and simple case studies Lepš et al. (2019) showed that species directional trends can  
184 mask year-to-year fluctuations among species. This has the potential to result in a biased  
185 estimation of asynchrony when using many widely used synchrony indices. Such  
186 directional trends could lead to either overestimation of year-to-year synchrony when  
187 the majority of species concomitantly increase or decrease over time, as well as  
188 overestimation of year-to-year asynchrony when some species increase and some others  
189 decrease over time.

190 Multiple indices have been developed to evaluate the level of synchrony among  
191 species in a community (Loreau & de Mazancourt 2008; Gross et al. 2014; Blüthgen et  
192 al. 2016; Lepš et al. 2018). Further methodologies have also been developed to assess  
193 directional trends, such as spectral or wavelet analyses, however, they are applicable  
194 only to very long or highly resolved time series (see Lepš et al. 2019 for an overview  
195 of these methods). None of the classically used synchrony indices disentangle, *a priori*,  
196 the actual year-to-year fluctuations from the directional trends. However, such indices  
197 can be ‘detrended’ using different methods (Wu et al. 2007; Lepš et al. 2019). One  
198 appealing a simple solution includes computing synchrony indices over moveable  
199 windows of three consecutive years (three-term local variance, ‘T3’, Hill 1973) instead  
200 of over the whole sampling period (Lepš et al. 2019). This ‘detrending’ approach, which  
201 we call T3 detrending approach, could allow testing the generality of the effect of  
202 directional trends on synchrony indices. If the focus of the research is on year-to-year  
203 fluctuations, then the minimum number of years to exclude trends and consider yearly  
204 fluctuations is 3 years, hence the three-term local variance. With bigger windows the  
205 computation of a common linear trend over the time window, and the focus on the  
206 deviation from this trend, does recall on the other method proposed by Lepš et al.  
207 (2019), using residuals of fitted linear models over a given time period. The first  
208 approach has the advantage that it can be computed with any existing index of  
209 synchrony and does not require the knowledge of the shape of possible linear trends in  
210 species abundance.

211 A widespread assessment of the effect of species directional trends on  
212 synchrony has been limited by the scarcity of available long-term data. Indeed, the  
213 study of temporal dynamics requires a substantial sampling effort to obtain meaningful  
214 data for temporal analyses. Although there are networks and independent groups with

215 long-term ecological data around the world, no major efforts have been made to compile  
216 and standardize the existing data in order to achieve a worldwide perspective.  
217 Consequently, a global-scale analysis would improve our understanding of both  
218 directional trends and year-to-year species fluctuations among the different synchrony  
219 indices and across diverse habitats, as well as how they are related with different types  
220 of disturbances or stressors. To face this challenge, we compiled plant community data  
221 from 77 temporal datasets with at least six sampling years, including almost 7800  
222 vegetation plots distributed across the world. First, we evaluated to what extent year-  
223 to-year synchrony could be masked by long-term trends, by using the T3 detrending  
224 approach for temporal series proposed by Lepš et al. (2019) on commonly used indices  
225 of synchrony. Second, we assessed whether synchrony patterns changed in plots in  
226 which initial conditions were maintained ('control') vs. plots in which new conditions  
227 were applied ('manipulated' plots, see methods), assuming that these new conditions  
228 would trigger compositional changes and therefore generate a trend. Third, we  
229 evaluated how detrended synchrony values are affected by the duration of the sampling.  
230 Finally, we asked if relationships that are commonly assessed in the literature regarding  
231 synchrony indices, i.e. the correlation between synchrony and species richness and the  
232 correlation between synchrony and community stability, changed markedly depending  
233 on whether the T3 detrending approach was applied. Additionally, beside the validation  
234 of the T3 approach introduced by Lepš et al. (2019), we further validated (using  
235 simulations) the functionality of the approach in the case of both monotonic and cyclical  
236 long-term trends and depending on the time series length (Appendix S1). We expect  
237 that: (1) directional trends in our datasets can overshadow either asynchrony or  
238 synchrony depending on the type of trend; (2) manipulative experiments can give rise  
239 to directional trends and therefore reinforce the need for detrended metrics to accurately

240 evaluate and compare community dynamics; (3) longer time series would provide  
241 greater chances to detect species directional trends; and (4) the presence of directional  
242 trends may affect the strength of the relationship between synchrony indices and species  
243 richness or community stability.

244 **Methods**

245 We collected 77 worldwide datasets of aboveground dry biomass, cover percentage, or  
246 frequencies of natural or semi-natural plant communities. These datasets consist of  
247 7788 permanent and semi-permanent plots sampled between 6 to 53 times over periods  
248 of 6 to 99 years. These datasets included plots with different treatments or  
249 manipulations. The plots were thus grouped into two categories: control vs.  
250 manipulated. In total 38 datasets presented both control and manipulated plots. Control  
251 includes those plots where the long-term conditions prior to the establishment of the  
252 sampling scheme were maintained throughout the sampling. For example, if the  
253 historical conditions in a given site include periodic mowing, this represents the  
254 ‘control’. The ‘manipulated’ plots were exposed to different treatments that altered the  
255 long-term conditions in their respective sites. These treatments included introduction or  
256 exclusion of grazing, mowing, removal of dominant species, fire, fertilization and  
257 climate change treatments. These wide categories allowed us to perform broad  
258 comparisons between different land-use and management conditions that are expected  
259 to influence species trends. The list of datasets, their characteristics in habitat,  
260 vegetation type and their available data on location and main manipulations is provided  
261 in Appendix S2.

262

263 *Synchrony measures*

264 For each of the 7788 plots, we computed the most common indices of community-level  
265 synchrony from existing literature. The main indices fall into two families. The first  
266 one is based on correlations between species’ abundances and includes two indices: the  
267 one proposed by Gross et al. (2014) and then this modified by Blüthgen et al. (2016),  
268 which weighs the contribution of species to community synchrony in terms of their

269 abundance. We call these indices ‘Gross’ and ‘GrossW’, respectively. The second  
270 family of indices is based on variance ratios, i.e. the variance in species fluctuations is  
271 compared against the null model of independent fluctuations of individual populations,  
272 and includes two indices: log variance ratio (‘Logvar’, Lepš et al. 2018) and  $\varphi$  (‘Phi’,  
273 Loreau & de Mazancourt 2008).

274 The Gross and GrossW indices range from -1 to +1 and Logvar from *-Inf* to  
275  $+\ln(nsp)$ , with *nsp* being the number of species in a community. High values indicate a  
276 common response of the species (synchrony), while any deviation from perfect  
277 synchrony indicates asynchrony; the lowest and negative values indicate that the  
278 increases or decreases in some species are compensated by opposite changes in others.  
279 For all, Gross, GrossW and Logvar, zero corresponds to a situation where the species  
280 fluctuate completely independently of each other. Finally, Phi ranges from 0 to 1, 1  
281 being perfect synchrony and any deviation from this value means asynchrony.

282 For each plot we also computed the average number of species in the plots  
283 across years, as well as the coefficient of variation (*CV*) of species abundances (standard  
284 deviation of the total sum of abundances or biomass across years divided by **the mean**  
285 **of** abundances or biomass across years). *CV* of total community abundance is a  
286 common measure of community (in)stability, where high values of *CV* indicate low  
287 stability in the community.

288 All measures of synchrony (and the *CV*) can be computed using the three-term  
289 local variance (*T3*; see Lepš et al. 2019 for an explanation of how to apply this method  
290 to the synchrony measures), originally introduced by Hill (1973) in the context of  
291 spatial pattern analysis. *T3* is then calculated as:

292

293

$$T3 = \frac{\sum_i^{n-2} (x_i - 2x_{i+1} + x_{i+2})^2}{6(n-2)}$$

294

295 where  $n$  is the number of years in the time-series,  $i$  is the year index, and  $x_i$  is the  
296 abundance recorded in year  $i$ . Consequently, T3 computes the variance by averaging  
297 variance estimates within a moving window of three consecutive years over the data.  
298 Any eventual increase in window size needs to be considered with respect to the limits  
299 imposed by total length of the series (Lepš 1990). In this context that the minimum  
300 length of the time series in our collection of datasets was 6 years, a movable window  
301 of 3 years seemed as a reasonable solution.

302 For the three-year window used in the calculations, the variance (which is  
303 needed in all existing index of synchrony) is estimated from the squared difference of  
304 the middle year and average of the years before and after. Therefore, if there is a perfect  
305 linear trend within these three years, the difference is zero. If there is no temporal trend  
306 in the time series analysed, then T3 is an estimate of classic variance (i.e. for long-time  
307 series without a trend the values of T3 and classical variance will converge; see below;  
308 Lepš et al. 2019). For each plot, each synchrony index (Gross, GrossW, Logvar and  
309 Phi) as well as the CV were calculated both with and without the T3 detrending method.

310

### 311 *Data analysis*

312 To assess to what extent the synchrony indices were affected by directional trends we  
313 followed different approaches. First, we correlated (across plots within each dataset)  
314 synchrony values with and without the T3 detrending approach. Specifically, for each  
315 dataset we retained a Rho coefficient from the Spearman correlation between indices  
316 calculated using the T3 detrending approach and their respective indices calculated  
317 without the T3 approach. Then, to test consistency across datasets another Spearman

318 test was run on the average of each synchrony index per dataset to test if the ranking in  
319 synchrony between datasets was maintained.

320         Second, we determined in how many datasets the T3 detrending approach  
321 significantly increased, or decreased, the synchrony values. For this we ran a series of  
322 paired t-tests, with a correction of the resulting p-values using the Benjamini–Hochberg  
323 approach (Benjamini & Hochberg 1995) for false discovery rates ( $n = 77$  tests for each  
324 index). To assess how the T3 detrending approach affected overall community stability,  
325 this test was also applied to the CV. For each of the assessed synchrony indices, we also  
326 retained for each dataset the t-statistic of the paired t-test, which indicates the strength  
327 and the direction of the effect (positive values implying T3 increased synchrony,  
328 negative ones when T3 decreased synchrony). Additionally, we evaluated how globally  
329 the synchrony values responded to the T3 detrending approach using Linear Mixed  
330 Models (LMM). In one approach, we computed for each plot two separate synchrony  
331 values (synchrony with and without the T3 detrending approach). The LMM contained  
332 one categorical variable (TraT3) as explanatory variable, specifying if the index was  
333 calculated with the T3 detrending approach or not. Plots nested in each dataset were  
334 considered as a random factor. Also, we computed for each plot the difference between  
335 the synchrony values with the T3 detrending approach and the values without it. Then,  
336 we evaluated how the effect of detrending (i.e. the difference between synchrony with  
337 and without T3) varied across habitat types and the biomes by fitting a LMM in which  
338 the dataset identity was considered as a random factor.

339         Third, we assessed whether synchrony values were affected by directional  
340 trends depending on the presence of an experimental manipulation changing abruptly  
341 the ecological conditions in a plot. To do this, we evaluated the effect of T3 using the  
342 t-statistic of the paired t-test within dataset (see above), separately in control and

343 manipulated plots within datasets. This analysis was restricted to those 38 datasets (out  
344 of 77) in which both control and manipulated plots were present and with at least three  
345 plots in each category. The same approach was used to test the effect of the duration  
346 (number of years) of the sampling period. This was undertaken using a linear model to  
347 test the relationship between the t-statistic (resulting from the paired-test) and number  
348 of years sampled in each dataset. We also used a similar LMM as described above to  
349 jointly evaluate the effects of the duration of the sampling period and experimental  
350 manipulation on the difference between the synchrony values with and without the T3  
351 detrending approach in these 38 datasets. In this model, we used the number of years  
352 of sampling, the experimental manipulation (manipulated vs. control plots) and their  
353 interaction as fixed factor, while each dataset was considered as a random factor. When  
354 a significant interaction was found, we split the database in control and manipulated  
355 plots and evaluated the effects of duration of the sampling period on both groups of  
356 plots.

357 Finally, to assess changes in strength of the commonly found ecological  
358 relationships involving synchrony with or without the use of the T3 detrending  
359 approach, we tested for each dataset using paired t-tests how strong were the (Pearson)  
360 correlations between synchrony and (i) species richness and (ii) community stability.  
361 For each of these two correlations, we considered the Pearson r and tested through a  
362 paired t-test if this r value (one for each dataset) was greater or smaller when using the  
363 T3 approach compared to when not using the T3 approach.

364 For simplicity, we mostly present the results of one index (GrossW) in the main  
365 text because it is widely applied in the literature. However, most of the results for the  
366 other indices considered are shown in Appendix (S3 and S4). Similarly, all results

367 concerning simulations are also included as Supporting Information material (Appendix  
368 S1). All the analysis were run in R (R Development Core Team 2018).

## 369 **Results**

370 The ranking of synchrony values with and without the T3 detrending approach was  
371 relatively consistent, both within and across datasets (Fig. 1). The Spearman Rho values  
372 computed within each of the 77 datasets were mostly positive and significant (Fig. 1a,  
373 for GrossW as an example; similar patterns were obtained for the other indices,  
374 Appendix S3). For example, in 44 out of the 77 datasets, the Spearman Rho was above  
375 0.5. This indicates a moderate correspondence in the ranking in synchronicity values  
376 across plots within datasets. Nevertheless, notable exceptions were present, for example  
377 in six datasets (~8% of the cases) Rho was below 0.1. However, in five out of these six  
378 datasets, either the number of manipulated plots was greater than the control plots, or  
379 the control plots were entirely absent. Overall, the Spearman ranking test done on the  
380 mean synchrony values indicated that greater synchrony without the T3 approach also  
381 provided greater synchrony with the T3 approach (Fig. 1b:  $Rho = 0.81$  and  $p < 0.001$ ).  
382 Most importantly, synchrony mean values were frequently greater where the T3  
383 detrending approach was applied than without its use (paired t-test  $p < 0.001$ ; Fig. 1b  
384 and Appendix S3).

385 We generally found a greater synchrony when accounting for long-term trends  
386 with the T3 methods than without. A significant increase in synchrony values was found  
387 for over 1/3 of the datasets (~30 datasets of 77, i.e. in ~40% of datasets synchrony  
388 significantly increase,  $p < 0.05$ , after correcting p-values for multiple tests with the  
389 Benjamini & Hochberg correction for false discovery rate within each synchrony index,  
390 Fig. 2; all significant tests reported in this section account for this p-value correction).  
391 Conversely, in around 10 datasets (13%, depending on the indices) synchrony values  
392 decreased using the T3 approach. In total around 50% of the datasets showed a  
393 significant change in synchrony values when using or not using the T3 detrending

394 approach. The pattern described for GrossW index was similar for all other synchrony  
395 indices. The number of datasets showing greater synchrony with the T3 approach was  
396 lower using Phi, which also showed a higher number of datasets showing lower  
397 synchrony with the T3 approach. In the majority of datasets (around 60) the CV  
398 computed using the T3 approach was significantly lower compared to the one computed  
399 without the T3 approach.

400         The LMM on the whole dataset showed a significant difference between the use  
401 of synchrony with and without the T3 detrending approach ( $p < 0.001$ ) with an overall  
402 increase in synchrony with T3, meaning that the T3 detrending approach generally led  
403 to increased synchrony values among all the plots (other synchrony indices yielded  
404 similar results). This result (which is similar to the significant deviation from the 1:1  
405 line in Fig. 1b mentioned above) further confirms that across the whole dataset long-  
406 term trends generally blur the importance of synchrony between species.

407         The results of the LMM evaluating the effects of habitat type and biomes on the  
408 T3 difference (i.e. on the difference between indices of synchrony with and without T3  
409 within a plot) showed a significant effect of the habitat type ( $\chi^2 = 47.21$ ;  $p < 0.001$ ), but  
410 no effect of the biomes. Grassland and savanna had in average positive values, meaning  
411 that a difference between T3 synchrony and synchrony without T3 were greater in these  
412 two habitats.

413         As expected, detrending had greater impacts on measures of synchrony in  
414 experimental plots than controls. Specifically evaluating ‘control’ vs. ‘manipulated’  
415 plots (using 38 datasets in which there were both types of plots), showed a greater  
416 number of cases in which the T3 approach produced significant changes in synchrony  
417 in the manipulated than in the control plots (Fig. 3 for the GrossW and Appendix S4  
418 for the other synchrony indices): 21 significant datasets (60%) in the manipulated plots

419 but only 10 (27%) in the control plots. Moreover, the effect of the sampling period  
420 length (number of years plots were sampled) was significantly related to the change in  
421 mean synchrony with the T3 approach only in the case of the manipulated plots (Fig. 3,  
422 using, as dependent variable, the t-values resulting by comparing synchrony with and  
423 without T3 approach using the paired t-tests within plot described above). Specifically,  
424 in the manipulated plots a longer sampling period improved the predictive ability of the  
425 effect of T3 approach on synchrony (increased detection of synchrony over long-term  
426 periods and increased detection of asynchrony in short-time periods). We confirmed  
427 these results using an LMM in which the difference of synchrony with and without T3  
428 were computed for each plot. This analyses showed a significant interaction between  
429 sampling period length and experimental manipulation. Sampling period length  
430 significantly increased the difference between synchrony values with and without the  
431 T3 approach only in manipulated plots ( $\chi^2 = 10.37$ ;  $p = 0.001$ ,  $n = 3414$ ).

432 Finally, we found that overall the relationships between synchrony and both  
433 species richness and community stability were similar (Appendix S5). Nevertheless  
434 there were slightly more frequent significant cases after detrending for Gross and  
435 GrossW (Appendix S5). For instance, the relationship between species richness and  
436 synchrony (i.e. when considering GrossW) was found significant in 15 and 11 datasets  
437 (out of 77) respectively when using or not using the T3 detrending approach (in both  
438 cases correcting for false discovery rates). However, this relationship, with LogVar,  
439 was found significant in 4 datasets less when using the T3. Further, with GrossW the  
440 expected positive relationship between synchrony and community CV was significant  
441 in 58 and 54 datasets while using or not using the T3 detrending, respectively (we did  
442 not detect significant negative relationship between CV and synchrony). The strength  
443 of these relationships, however, was not affected by the detrending approach. In neither

444 the (i) species richness and synchrony correlations, nor the (ii) community CV and  
445 synchrony correlations, did we detect significant differences when using or not using  
446 the T3 detrending approach (in both cases  $p > 0.2$ ). This implies that the use of the T3  
447 detrending approach did not systematically produce greater or weaker correlations  
448 when analyzing these common relationships.

449 **Discussion**

450 In this study we show that the synchrony patterns usually attributed to compensatory  
451 dynamics could be actually caused by trends in species composition. Without  
452 accounting for these trends effectively, it is possible that compensatory effects could be  
453 generally overemphasized (in 30% of our datasets) or even underemphasized (in 10%  
454 of our datasets). Previous studies of synchrony and compensatory dynamics have often  
455 overlooked the possible effects of directional trends on the studied communities. Only  
456 few studies, such as Vasseur and Gaedke (2007), Loreau & de Mazancourt (2008) and  
457 Tredennick et al. (2017), have effectively filtered out species trends (using wavelet  
458 based methods or considering growth rates of species in time, instead of raw  
459 abundances). Long-term trends in abundances, either directional or cyclical, indeed  
460 have the potential to bias the interpretation of synchrony with the most commonly used  
461 indices. The T3 detrending approach can account for this bias (see simulation in Lepš  
462 et al. 2019 and in Appendix S1). The advantages of the T3 approach, compared to other  
463 approaches, are its lower data requirement and consideration of all species in a  
464 community, not just the most frequent ones (Lepš et al. 2019).

465 In ~40% of the datasets, and in the overall model across all plots, synchrony  
466 using the T3 detrending approach was significantly greater than synchrony without  
467 using it (Fig. 2). The ~40% estimate is, furthermore, a conservative one as we account  
468 for Type I errors. Overall, the mean values of synchrony computed with the T3  
469 detrending approach were higher than without it in the majority of cases, both within  
470 and across datasets (Fig. 1b, and LMM). This is an important finding because it suggests  
471 that our appreciation of the importance of asynchrony, and therefore compensatory  
472 dynamics, may have been possibly overestimated, leading to wrong conclusions about  
473 synchrony-asynchrony in communities. These findings highlight the necessity of

474 evaluating the effects of possible directional trends on synchrony to accurately estimate  
475 the importance of ecological mechanisms regulating compensatory dynamics. The  
476 difference between the indices calculated using T3 detrending approach and without it  
477 were higher in grasslands and meadows, possibly because in the absence of slow-  
478 growing, less dynamic, woody species. In these communities temporal trends can thus  
479 be more easily detected compared to other types of vegetation. The increase in  
480 synchrony after detrending also suggests the presence of opposite trends of species  
481 abundances in time, such as when one species is decreasing steadily and another  
482 increasing. For example, trends could be the result of species responding differently to  
483 disturbance or to an increase in nutrient availability. Such opposite trends could be  
484 monotonic or following waves in time (Wu et al. 2007), e.g. resulting from periodic  
485 climate events such as “El Niño”, or intrinsic cycling of particular functional groups  
486 such as legumes (Herben et al. 2017). These results are partially expected because our  
487 datasets comprised natural or semi-natural well-established plant communities but  
488 included experimental conditions in which changes in abundance or composition of  
489 species are common.

490         When considering datasets with both control and manipulated plots (~50% of  
491 the datasets) the effect of the T3 approach was more frequently significant in  
492 manipulated plots than in control plots (Fig. 3). These plots were more prone to be  
493 affected by a directional trend promoted by the specific manipulation imposed. This  
494 result agrees with our hypothesis that events like soil-nutrient alteration (e.g. by  
495 fertilization) and recovery from disturbance might promote directional trends. This  
496 result was expected as some of the experimental manipulations were designed to  
497 directly alter species composition, in order to test their effects on community  
498 synchrony. However, such prompted changes, often due to colonization-competition

499 trade-offs in species composition, can mask year-to-year fluctuations, and hence these  
500 experiments should disentangle these biologically different effects on synchrony. For  
501 these reasons, we recommend that any index of synchrony should be computed with  
502 and without the T3 approach to properly evaluate the corresponding effects of long-  
503 term experimental treatments and year-to-year fluctuations. Our result reinforces the  
504 assumption that the effect of the T3 approach could be stronger in changing  
505 environments/communities and the combination of indices with and without the T3  
506 approach can be important to distinguish the mechanisms causing differential long-term  
507 species responses to changes in environmental conditions from the differential species  
508 responses to short-term species fluctuations on synchrony/asynchrony relationships.

509         The effect of detrending on synchrony values was particularly pronounced in  
510 the case of succession. During succession the majority of species will increase their  
511 abundance, which will cause them to be ultimately positively correlated in time.  
512 However, these same species can compensate each other or vary independently on a  
513 year-by-year basis, even if they all generally increase in time, so the existing synchrony  
514 indices would tend to overestimate their actual year-to-year synchrony between species  
515 within such communities. In fact, among the seven datasets with a Rho below 0.1 (Fig.  
516 1a), the majority were characterised by being exposed to intense disturbance regimes  
517 that triggered some type of successional process. For instance, plots of four datasets  
518 had been exposed to a fire before or during the experiment, and two evaluated the effect  
519 of herbivory exclusion (where the reduction in grazing intensity allowed the  
520 development of higher vegetation like shrubs and trees). Both treatments are good  
521 examples of environmental conditions promoting species directional trends (Pardo et  
522 al. 2015) and thus affect synchrony values.

523           Interestingly, the effect of the T3 approach on the synchrony measured in  
524 manipulated plots depended on the period length of the sampling scheme. Manipulated  
525 plots sampled over longer time periods revealed higher synchrony values when using  
526 the T3 detrending approach (Fig. 3). In other words, the longer is the sampling period  
527 the greatest chance that there is a difference between T3 synchrony and synchrony  
528 without T3 in manipulated plots. Longer time series likely increased the chances that  
529 some species will have opposite trends in response to manipulation, with some  
530 increasing over time and others decreasing. In a shorter time series, on the contrary, the  
531 time lag in species responses (particularly extinction debt, Helm, Hanski, & Partel  
532 2006; Lepš 2014) could cause that some species increase quickly in response to  
533 manipulation, while others might respond more slowly. The T3 detrending approach,  
534 therefore, will affect those species with a similar temporal trend in response to short-  
535 term manipulations. Consequently, the duration of the sampling period stands out as a  
536 key factor in the evaluation of temporal dynamics. We showed that, in the case of  
537 manipulated communities, classical methods tended to overestimate year-to-year  
538 synchrony when the sampling period was shorter, and underestimate it when the  
539 sampling period was longer. This highlights the importance of T3 approach for a correct  
540 evaluation of year-to-year synchrony between species. However, further research is  
541 required to find the causes and consequences of these results.

542           Finally, we generally found that the T3 detrending approach did not cause strong  
543 changes in the correlation between synchrony and both species richness and community  
544 stability, two of the most iconic relationships in temporal dynamics studies (Hautier et  
545 al. 2014; Blüthgen et al. 2016). However, there were more cases of significant  
546 correlations with the T3 approach and strength of the correlations could vary  
547 considerably (i.e.  $R < 0.6$ ) across datasets. In summary, this suggests that while the

548 applications of the T3 detrending approach did not produce systematically greater or  
549 weaker correlations on commonly used tests in ecology, the strength of the relationships  
550 could differ. These results confirm that the use of T3 approach to detrend the synchrony  
551 indices is far from trivial. As such, the conclusions obtained previously from studies  
552 that did not apply the method are not necessarily incorrect. Therefore, applying the  
553 detrended and non-detrended methods in a complementary way might bring us closer  
554 to understanding the directional changes in community dynamics. For instance,  
555 divergent trends, e.g. due to differential response to global warming with some species  
556 increasing and other decreasing, might stabilize communities and could maintain  
557 ecosystem functions unaltered in response to global warming, even if there are no short-  
558 term compensatory mechanisms between species. Hence, it is important to consider  
559 both the synchrony with and without detrending approach for teasing apart different  
560 causes of stability, or instability, in response to global change drivers.

561         The evaluation of synchrony with the T3 detrending method provides a feasible  
562 measure to reveal year-to-year fluctuations of species by removing the effect of  
563 directional trends. In comparison to methods using species growth rates, the T3  
564 approach can be important because it enables the evaluation of the indices with and  
565 without the approach and also accounts for species which are not dominant and/or less  
566 frequent (in the case of the growth rates, log-transformation is needed, which might not  
567 be advisable in the case of zero abundances in specific years). This method has the  
568 advantage of evaluating both monotonic and non-monotonic directional trends, and can  
569 thus be used to detect year-to-year fluctuations in the face of cyclical periods, such as  
570 alternation between drought-wet periods (e.g. Riginos et al. 2018).

571 **Acknowledgements**

572 We thank multiple entities for the financial support necessary to obtain the different  
573 databases: the U.S. National Science Foundation under grant numbers DEB-8114302,  
574 DEB-8811884, DEB-9411972, DEB-0080382, DEB-0620652, DEB-1234162, DEB-  
575 9707477, DEB-0316402, DEB-08-16453, and DEB-12-56034, DEB-0618210, the  
576 Nutrient Network (<http://www.nutnet.org>) experiment from the National Science  
577 Foundation Research Coordination Network (NSF-DEB-1042132), the New Zealand  
578 National Vegetation Survey Databank, the Spanish MINECO (Project CGL2014-  
579 53789-R), the Madrid Regional Government (Projects REMEDINAL-3 and  
580 REMEDINAL-TE), the European Research Council Synergy grant 610028  
581 (IMBALANCE-P), the Institute on the Environment (DG-0001-13), the SOERE-  
582 ACBB financed through French National Agency for Research (ANAAEE, ANR-11-  
583 INBS-0001), the Estonian Research Council (IUT 20-28, IUT 20-29), Czech Science  
584 Foundation (GAČR 17-05506S), the European Regional Development Fund (Centre of  
585 Excellence EcolChange), the German Federal Environmental Foundation (DBU) for a  
586 grant to the NABU Hamburg (management experiment *Calamagrostis epigejos*), and  
587 the German Federal Ministry of Education and Research within the framework of the  
588 project BIOTA Southern Africa (promotion numbers 01LC0024, 01LC0024A and  
589 01LC0624A2), Task 159 of SASSCAL (promotion number 01LG1201) and the  
590 Scottish Government's Rural and Environmental Science and Analytical Services  
591 division. Acknowledgement Data owned by NERC<sup>©</sup> Database Right/Copyright NERC.  
592 Further support was provided by the Jornada Basin Long-Term Ecological Research  
593 (LTER) project, Cedar Creek Ecosystem Science Reserve and the University of  
594 Minnesota. We also thank the Lawes Agricultural Trust and Rothamsted Research for  
595 data from the e-RA database. The Rothamsted Long-term Experiments National  
596 Capability (LTE-NCG) is supported by the UK Biotechnology and Biological Sciences  
597 Research Council (Grant BBS/E/C/000J0300) and the Lawes Agricultural Trust.

598

599

600 **Author contributions:** F.B., L.G. and J.L. conceived the project. All authors but E.V.,  
601 F.B., T.G and L.G. collected the data used in this analysis. E.V. and T.G. assembled  
602 data. F.B. performed the analyses. E.V. and F.B. wrote the first draft of the manuscript  
603 and all the authors (especially L.G. and J. L.) contributed substantially to the revisions.

604

605 **Data accessibility**

606 The data that support the findings of this study are available at Figshare (Valencia et al.  
607 2019).

608

609 **References**

610

- 611 Benjamini, Y., & Hochberg, Y. 1995. Controlling the False Discovery Rate: A  
612 Practical and Powerful Approach to Multiple Testing. *Journal of the Royal*  
613 *Statistical Society: Series B (Methodological)* 57: 289–300.
- 614 Blüthgen, N., Simons, N.K., Jung, K., Prati, D., Renner, S.C., Boch, S., Fischer, M.,  
615 Hölzel, N., Klaus, V.H., Kleinebecker, T., Tschapka, M., Weisser, W.W., &  
616 Gossner, M.M. 2016. Land use imperils plant and animal community stability  
617 through changes in asynchrony rather than diversity. *Nature Communications* 7:  
618 10697.
- 619 Cardinale, B., Wright, J., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S.,  
620 Loreau, M., & Weis, J.J. 2007. Impacts of plant diversity on biomass production  
621 increase through time because of species complementarity. *Proceedings of the*  
622 *National Academy of Sciences of the United States of America* 104: 18123–  
623 18128.
- 624 Craven, D., Eisenhauer, N., Pearse, W.D., Hautier, Y., Isbell, F., Roscher, C., Bahn,  
625 M., Beierkuhnlein, C., Bönisch, G., Buchmann, N., Byun, C., Catford, J.A.,  
626 Cerabolini, B.E.L., Cornelissen, J.H.C., Craine, J.M., De Luca, E., Ebeling, A.,  
627 Griffin, J.N., Hector, A., Hines, J., Jentsch, A., Kattge, J., Kreyling, J., Lanta, V.,  
628 Lemoine, N., Meyer, S.T., Minden, V., Onipchenko, V., Polley, H.W., Reich,  
629 P.B., van Ruijven, J., Schamp, B., Smith, M.D., Soudzilovskaia, N.A., Tilman,  
630 D., Weigelt, A., Wilsey, B., & Manning, P. 2018. Multiple facets of biodiversity  
631 drive the diversity–stability relationship. *Nature Ecology and Evolution* 2: 1579–  
632 1587.
- 633 Gonzalez, A., & Loreau, M. 2009. The causes and consequences of compensatory  
634 dynamics in ecological communities. *Annual Review of Ecology, Evolution, and*  
635 *Systematics* 40: 393–414.
- 636 Gross, K., Cardinale, B.J., Fox, J.W., Gonzalez, A., Loreau, M., Wayne Polley, H.,  
637 Reich, P.B., & van Ruijven, J. 2014. Species richness and the temporal stability  
638 of biomass production: a new analysis of recent biodiversity experiments. *The*  
639 *American Naturalist* 183: 1–12.
- 640 Hautier, Y., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S., Hillebrand, H.,  
641 Lind, E.M., MacDougall, A.S., Stevens, C.J., Bakker, J.D., Buckley, Y.M., Chu,  
642 C., Collins, S.L., Daleo, P., Damschen, E.I., Davies, K.F., Fay, P.A., Firn, J.,  
643 Gruner, D.S., Jin, V.L., Klein, J.A., Knops, J.M.H., La Pierre, K.J., Li, W.,  
644 McCulley, R.L., Melbourne, B.A., Moore, J.L., O’Halloran, L.R., Prober, S.M.,  
645 Risch, A.C., Sankaran, M., Schuetz, M., & Hector, A. 2014. Eutrophication  
646 weakens stabilizing effects of diversity in natural grasslands. *Nature* 508: 521–  
647 525.
- 648 Helm, A., Hanski, I., & Partel, M. 2006. Slow response of plant species richness to  
649 habitat loss and fragmentation. *Ecology Letters* 9: 72–77.
- 650 Herben, T., Mayerová, H., Skálová, H., Hadincová, V., Pecháčková, S., & Krahulec,  
651 F. 2017. Long-term time series of legume cycles in a semi-natural montane  
652 grassland: evidence for nitrogen-driven grass dynamics? (R. Ostertag, Ed.).  
653 *Functional Ecology* 31: 1430–1440.
- 654 Hill, M.O. 1973. The Intensity of spatial pattern in plant communities. *The Journal of*  
655 *Ecology* 61: 225.

- 656 Houlahan, J.E., Currie, D.J., Cottenie, K., Cumming, G.S., Ernest, S.K.M., Findlay,  
657 C.S., Fuhlendorf, S.D., Gaedke, U., Legendre, P., Magnuson, J.J., McArdle,  
658 B.H., Muldavin, E.H., Noble, D., Russell, R., Stevens, R.D., Willis, T.J.,  
659 Woiwod, I.P., & Wondzell, S.M. 2007. Compensatory dynamics are rare in  
660 natural ecological communities. *Proceedings of the National Academy of*  
661 *Sciences* 104: 3273–3277.
- 662 Hubbell, S.P. 2001. *The unified neutral theory of biodiversity and biogeography*.  
663 Princeton University Press.
- 664 Lepš, J. 1990. Comparison of transect methods for the analysis of spatial pattern.  
665 *Spatial processes in plant communities* 71–82.
- 666 Lepš, J. 2014. Scale- and time-dependent effects of fertilization, mowing and  
667 dominant removal on a grassland community during a 15-year experiment (S.  
668 Wan, Ed.). *Journal of Applied Ecology* 51: 978–987.
- 669 Lepš, J., Götzenberger, L., Valencia, E., & de Bello, F. 2019. Accounting for long-  
670 term directional trends on year-to-year synchrony in species fluctuations.  
671 *Ecography* 42: 1728–1741.
- 672 Lepš, J., Májeková, M., Vítová, A., Doležal, J., & de Bello, F. 2018. Stabilizing  
673 effects in temporal fluctuations: management, traits, and species richness in high-  
674 diversity communities. *Ecology* 99: 360–371.
- 675 Loreau, M., & de Mazancourt, C. 2013. Biodiversity and ecosystem stability: a  
676 synthesis of underlying mechanisms (E. Duffy, Ed.). *Ecology Letters* 16: 106–  
677 115.
- 678 Loreau, M., & de Mazancourt, C. 2008. Species synchrony and its drivers: neutral and  
679 nonneutral community dynamics in fluctuating environments. *The American*  
680 *Naturalist* 172: E48–E66.
- 681 Milchunas, D., Lauenroth, W., & Burke, I. 1998. Livestock grazing: animal and plant  
682 biodiversity of shortgrass steppe and the relationship to ecosystem function.  
683 *Oikos* 83: 65–74.
- 684 Pardo, I., Doak, D.F., García-González, R., Gómez, D., & García, M.B. 2015. Long-  
685 term response of plant communities to herbivore exclusion at high elevation  
686 grasslands. *Biodiversity and Conservation* 24: 3033–3047.
- 687 R Development Core Team. 2018. *R: A language and environment for statistical*  
688 *computing* (A. R Foundation for Statistical Computing, Vienna, Ed.). R  
689 Foundation for Statistical Computing, Vienna, Austria.
- 690 Rabotnov, T.A. 1974. Differences Between Fluctuations and Successions. In  
691 *Vegetation Dynamics*, pp. 19–24. Springer Netherlands, Dordrecht.
- 692 Riginos, C., Porensky, L.M., Veblen, K.E., & Young, T.P. 2018. Herbivory and  
693 drought generate short-term stochasticity and long-term stability in a savanna  
694 understory community. *Ecological Applications* 28: 323–335.
- 695 Silvertown, J., Poulton, P., Johnston, E., Edwards, G., Heard, M., & Biss, P.M. 2006.  
696 The Park Grass Experiment 1856–2006: its contribution to ecology. *Journal of*  
697 *Ecology* 94: 801–814.
- 698 Stevens, C., Duprè, C., Gaudnik, C., Dorland, E., Dise, N., Gowing, D., Bleeker, A.,  
699 Alard, D., Bobbink, R., Fowler, D., Vandvik, V., Corcket, E., Mountford, J.O.,  
700 Aarrestad, P.A., Muller, S., & Diekmann, M. 2011. Changes in species  
701 composition of European acid grasslands observed along a gradient of nitrogen

702 deposition. *Journal of Vegetation Science* 22: 207–215.

703 Tilman, D., Isbell, F., & Cowles, J.M. 2014. Biodiversity and ecosystem functioning.  
704 *Annual Review of Ecology, Evolution, and Systematics* 45: 471–493.

705 Tomimatsu, H., Sasaki, T., Kurokawa, H., Bridle, J.R., Fontaine, C., Kitano, J.,  
706 Stouffer, D.B., Vellend, M., Martijn Bezemer, T., Fukami, T., Hadly, E.A., Van  
707 Der Heijden, M.G.A., Kawata, M., Efi, S.K., Kraft, N.J.B., Mccann, K.S.,  
708 Mumby, P.J., Nakashizuka, T., Petchey, O.L., Romanuk, T.N., Suding, K.N.,  
709 Takimoto, G., Urabe, J., & Yachi, S. 2013. Sustaining ecosystem functions in a  
710 changing world: a call for an integrated approach. *Journal of Applied Ecology*  
711 50: 1124–1130.

712 Tredennick, A.T., de Mazancourt, C., Loreau, M., & Adler, P.B. 2017. Environmental  
713 responses, not species interactions, determine synchrony of dominant species in  
714 semiarid grasslands. *Ecology* 98: 971–981.

715 Valencia, E., de Bello, F., Lepš, J., Galland, T., E-Vojtkó, A., Conti, L., Danihelka, J.,  
716 Dengler, J., Eldridge, D.J., Estiarte, M., García-González, R., Garnier, E.,  
717 Gómez, D., Harrison, S., Herben, T., Ibáñez, R., Jentsch, A., Juergens, N.,  
718 Kertész, M., Klumpp, K., Louault, F., Marrs, R.H., Ónodi, G., Pakeman, R.J.,  
719 Pärtel, M., Peco, B., Peñuelas, J., Rueda, M., Schmidt, W., Schmiedel, U.,  
720 Schuetz, M., Skalova, H., Šmilauer, P., Šmilauerová, M., Smit, C., Song, M.,  
721 Stock, M., Val, J., Vandvik, V., Wesche, K., Woodcock, B.A., Young, T.P., Yu,  
722 F., Zobel, M., Götzenberger, L. 2020. Data from “Directional trends in species  
723 composition over time can lead to a widespread overemphasis of year-to-year  
724 asynchrony”. Figshare. [https://doi.org/ 10.6084/m9.figshare.8276309](https://doi.org/10.6084/m9.figshare.8276309).

725 Vasseur, D.A., & Gaedke, U. 2007. Spectral analysis unmask synchronous and  
726 compensatory dynamics in plankton communities. *Ecology* 88: 2058–2071.

727 Walter, J.A., Ives, A.R., Tooker, J.F., & Johnson, D.M. 2018. Life history and habitat  
728 explain variation among insect pest populations subject to global change.  
729 *Ecosphere* 9: e02274.

730 Wu, Z., Huang, N.E., Long, S.R., & Peng, C.-K. 2007. On the trend, detrending, and  
731 variability of nonlinear and nonstationary time series. *Proceedings of the*  
732 *National Academy of Sciences of the United States of America* 104: 14889–  
733 14894.

734

735

736 **Figure legend**

737

738 **Figure 1.** Effects of the T3 detrending approach on synchrony, using the GrossW index  
739 (Blüthgen et al. 2016) as an example. In panel (a), a ranking correlation between  
740 synchrony values with and without detrending was computed for each of the 77 datasets  
741 considered. The histogram reports the 77 Rho values of the Spearman ranking  
742 correlations. Panel (b) reports, for each of the 77 datasets, the mean (+/- standard error)  
743 of the synchrony values with and without the T3 detrending approach. Vertical and  
744 horizontal dashed lines indicate zero synchrony (i.e. absence of synchrony). The solid  
745 line represents the 1:1 line above which, for example T3 synchrony was greater than  
746 synchrony without T3.

747

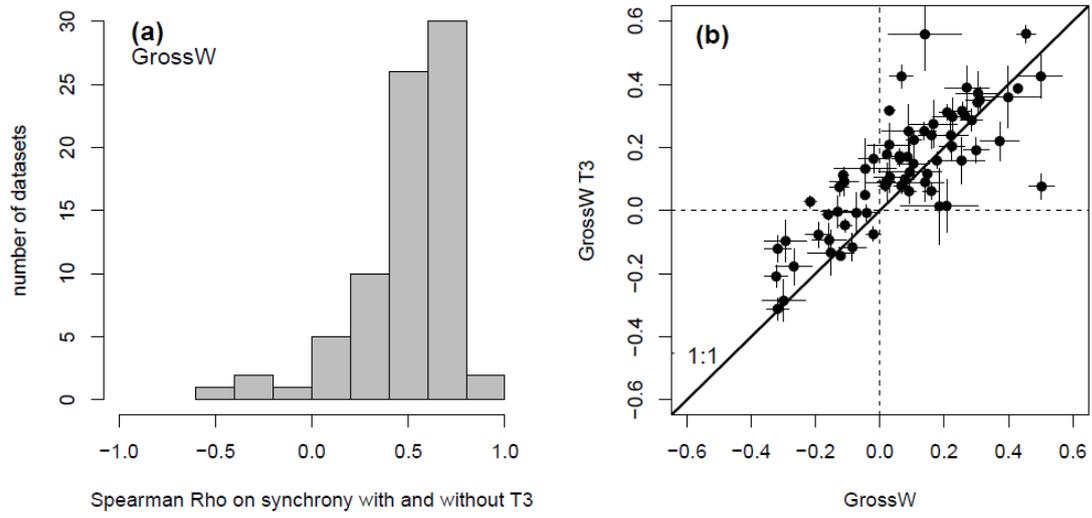
748 **Figure 2.** Summary of the directional effects of the T3 detrending approach on various  
749 synchrony indices and on CV. The bar plots indicate the numbers of datasets (n=77) in  
750 which the T3 approach significantly increased (red bars) or decreased (blue bars)  
751 synchrony values using a paired t-test after correction for false discovery rates. Grey  
752 bars indicate the number of datasets with non-significant paired t-tests.

753

754 **Figure 3.** Effects of the T3 detrending approach in manipulated vs. control plots. The  
755 plots report results of t-tests on 38 datasets in which there were both manipulated and  
756 control plots. For each dataset we used a pairwise t-test to compare synchrony values  
757 (using the GrossW synchrony index, Blüthgen et al. 2016) with and without the T3  
758 approach (a: manipulated plots, and b: control plots). Positive values of the t-statistic  
759 indicate that the T3 approach increased synchrony and negative ones indicate that the  
760 T3 decreased synchrony. Values outside the grey area in each plot indicate significant  
761 t-tests after correction for false discovery rates ('ns' indicates  $p > 0.05$ ). For each panel  
762 an  $R^2$  for the relationship between t-statistic and number of years sampled in each  
763 dataset is provided together with the p-value of the regression model (the corresponding  
764 regression line is shown when significant). Syn: Synchrony.

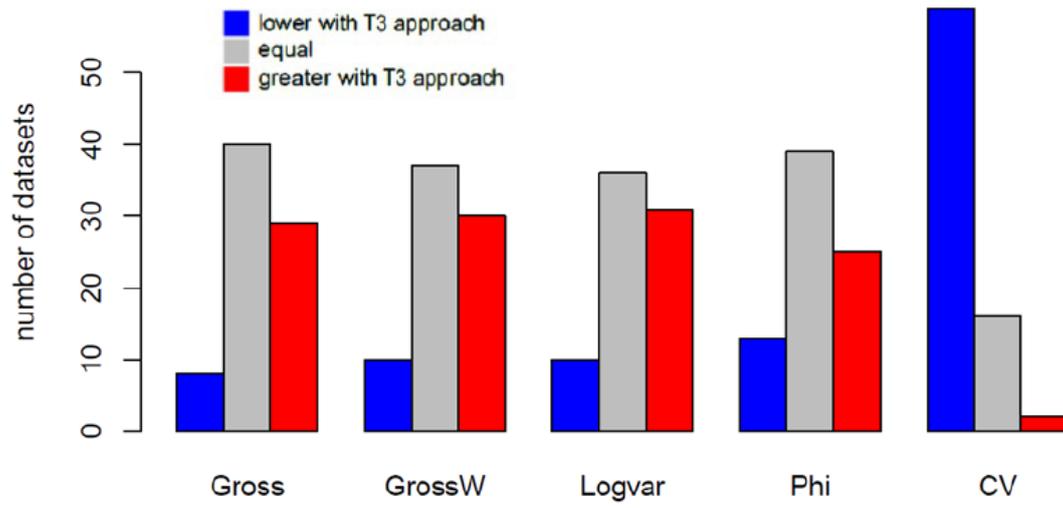
765

766 **Figure 1.**  
767



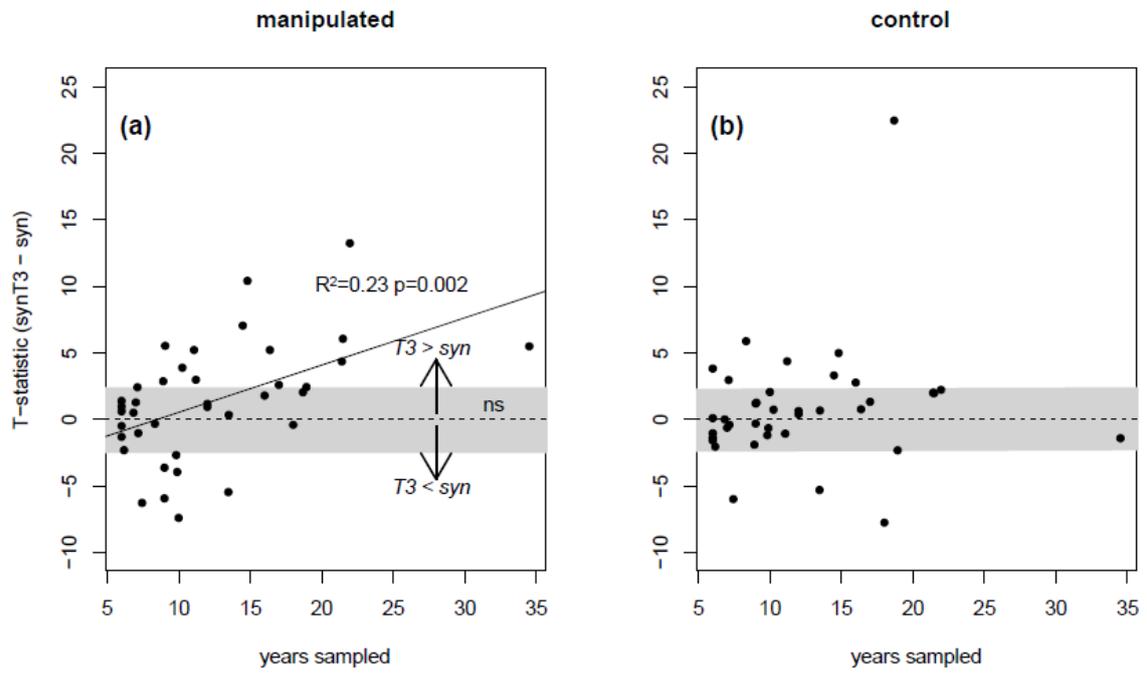
768

769 **Figure 2.**  
770



771

772 **Figure 3.**  
773



774

775 **Supporting Information**

776 Additional Supporting Information may be found in the online version of this article:  
777

778 **Appendix S1.** Simulating long term trends in artificial communities to validate  
779 effectiveness of the T3 approach

780 **Appendix S2.** Descriptions of each dataset, highlighting the treatments of the datasets  
781 with ‘control’ and ‘manipulated’ plots.

782 **Appendix S3.** Application of the analyses shown in Fig. 1 of the main text to the  
783 three remaining indices of synchrony.

784 **Appendix S4.** Application of the analyses shown in Fig. 3 of the main text to the  
785 three remaining indices of synchrony.

786 **Appendix S5.** Results of the correlation between synchrony indices with species  
787 richness or with the CV of total abundance.

1 Supporting Information to the paper  
2 Valencia et al. Directional trends in species composition over time can lead to a  
3 widespread overestimation of asynchrony. *Journal of Vegetation Science*.  
4  
5 **Appendix S1.** *Simulating long term trends in artificial communities to validate*  
6 *effectiveness of the T3 approach*

7 We created artificial temporal community data with desired patterns of temporal  
8 fluctuations (prevailing synchrony or asynchrony) using the “syngenr” R function  
9 (Lepš et al. 2019). This function offers the possibility to build simulated communities,  
10 fixing some parameters, such as the years of the time series (100 years) and the  
11 number of species (8 species). Once the communities were established, communities  
12 fluctuating in time were created according to the following scenarios: prevailing  
13 synchrony or prevailing asynchrony. A synchronous pattern was simulated by having  
14 a common response for all species to a hypothetical environmental cue. Accordingly,  
15 an asynchronous pattern was created by having half of the species responding  
16 positively and the other half negatively to the environmental cue. Furthermore, we  
17 simulated directional (monotonic) and cyclical long term trends for these artificial  
18 communities. First, we simulated a case where most species had a common long-term  
19 positive trend (monotonic) leading to a steady increase of individual species over  
20 time. This would lead to detect synchrony with the synchrony indices (unmodified),  
21 even if the species are actually behaving asynchronous. Second, we simulated the  
22 opposite case, where species either increase or decrease in time, with the  
23 increase/decrease for each species defined by a combined bimodal distribution from  
24 two normal distributions with -1 and 1 as means, and random subset from half of the  
25 species more probably have a positive long-term trend and the other half of the  
26 species more probably a negative long-term trend. Finally, we simulated a case were  
27 the directional long-term had cyclical tendencies. The cyclical long term trends were

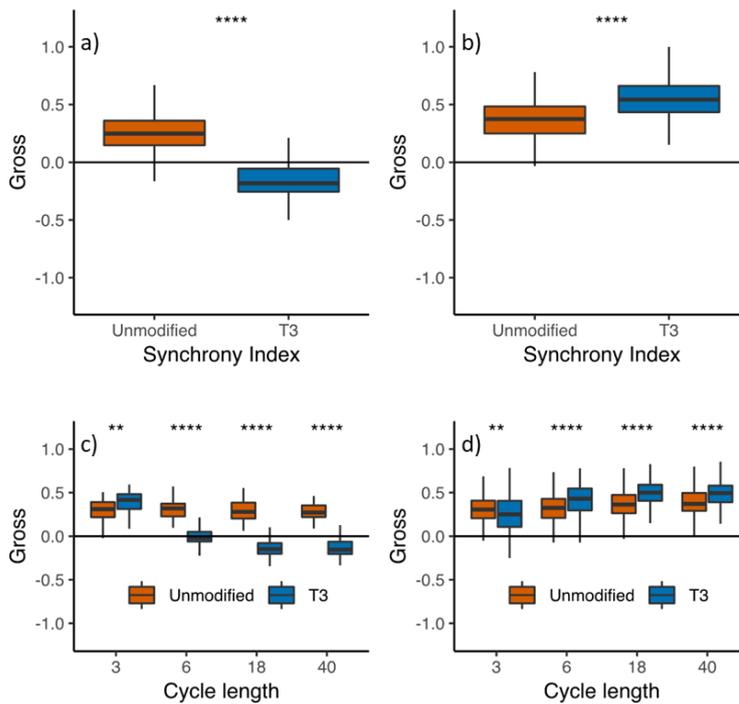
28 evaluated with different cycle length: 3, 6, 18 and 40 years. These cycle lengths  
29 reflect some known potential long term cycles that drive communities across the  
30 world, such as the El Niño Oscillation or Pacific Decadal Oscillation, which have  
31 intervals of 3-6 years and 10-20 year, respectively. In summary, we simulated two  
32 scenarios of year-to-year species fluctuations (prevailing synchrony or prevailing  
33 asynchrony) and three types of long-term directional trends (i.e. monotonic with a  
34 common or contrasted trend, and cyclical trends), resulting in six possible  
35 combinations of trend–fluctuation scenarios. In all these simulated communities, we  
36 calculated the different synchrony indices (Gross, GrossW, Logvar and Phi), with or  
37 without the use of the T3 detrending approach, using the “calc\_sync” R function  
38 (Lepš et al. 2019).

39 We assessed the effectiveness of the T3 detrending approach when long-term  
40 monotonic or cyclical trends are present in the data across the most common  
41 synchrony indices, using a paired t-test. Fluctuations simulated under scenarios of  
42 long-term trends in species abundances showed biased index estimates, i.e. the  
43 simulated synchrony or asynchrony patterns were overshadowed by the patterns  
44 caused by long-term trends. In the case of species having long-term directional or  
45 cyclical trends, asynchrony was masked by the synchrony (Figure Appendix S1a and  
46 S1c). Then, the synchrony indices without the T3 detrending approach were not able  
47 to detect asynchrony, even if the species were actually behaving asynchronously.  
48 These synchrony indices values were significantly higher than those with the T3  
49 detrending approach. These biases were found across all indices but the application of  
50 the T3 detrending approach was correctly able to remove them, in all indices (Figure  
51 Appendix S1). In the opposite case, simulation of synchrony together with long-term  
52 monotonic or cyclical trends, the difference still prevailed among the synchrony with

53 and without the T3 detrending approach, but with a less pronounced effect (Figure  
 54 Appendix S1b and S1d).

55  
 56 **Figure Appendix S1.** Results of synchrony indices (Gross, GrossW Logvar, and Phi)  
 57 (Loreau & de Mazancourt 2008; Gross et al. 2014; Blüthgen et al. 2016; Lepš et al.  
 58 2018), with or without the use of the T3 detrending approach, in artificial temporal  
 59 communities where long term trends were simulated. The panels report results for a  
 60 common long-term directional trend (a) (i.e. creating synchrony; all species increasing  
 61 in time), a contrasted long-term trend (b) (i.e. half species increasing, the other half  
 62 decreasing, creating asynchrony) and a cyclical trend (c and d). Within each of these  
 63 scenarios we considered two scenarios: year to year asynchrony (a and c) and  
 64 synchrony (b and d). The cyclic trends also included different cycle length (3, 6, 18  
 65 and 40 years). The created communities had a total of 8 species. Asterisks above and  
 66 between boxes depict significant differences among the synchrony indices with or  
 67 without the T3 approach as assessed with a paired t-test. \*:  $P < 0.05$ ; \*\*:  $P < 0.01$ ;  
 68 \*\*\*:  $P < 0.001$ ; \*\*\*\*:  $P < 0.0001$ .

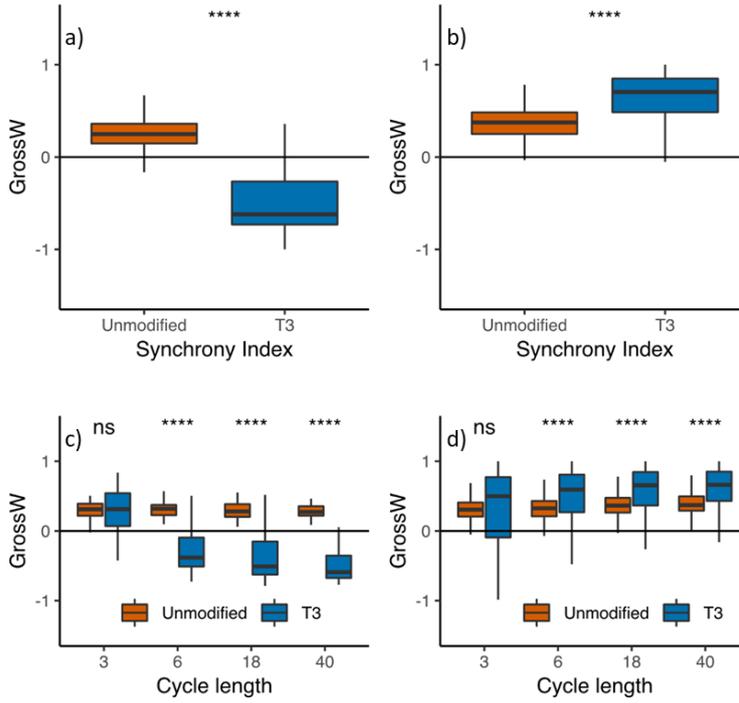
69  
 70 **Gross**



71  
 72

73 **GrossW**

74

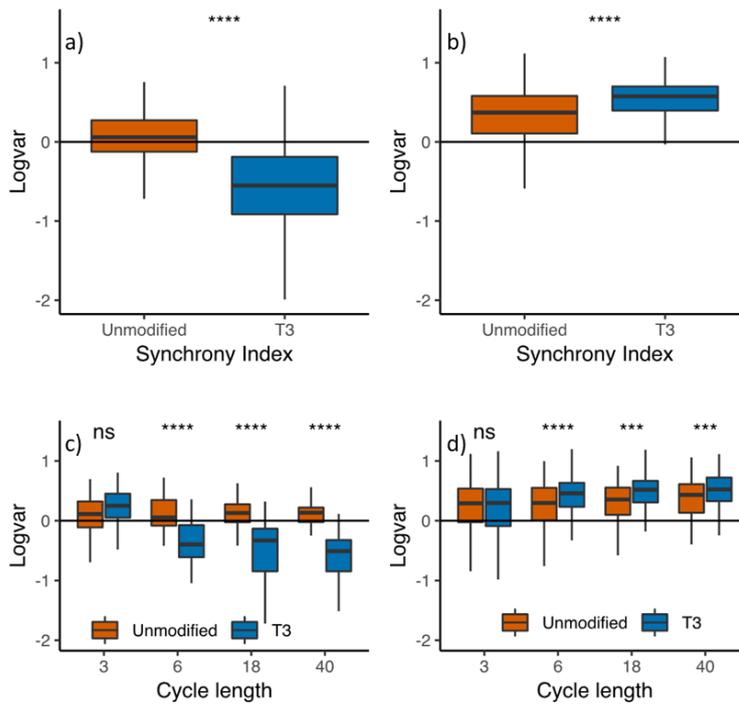


75

76

77 **Logvar**

78

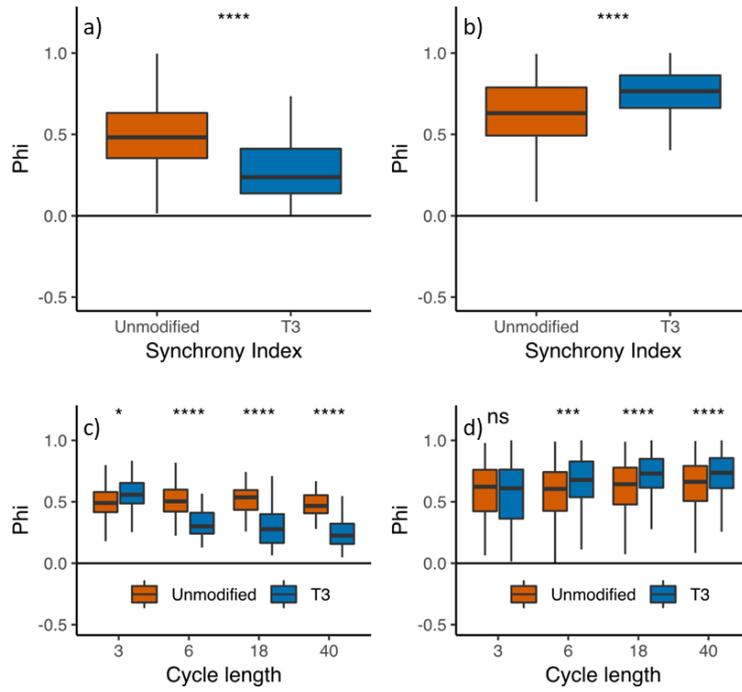


79

80

81

82 **Phi**  
83



84  
85

86 Supporting Information to the paper  
87 Valencia et al. Directional trends in species composition over time can lead to a  
88 widespread overestimation of asynchrony. *Journal of Vegetation Science*.  
89

90 **Appendix S2.** Descriptions of each dataset, highlighting the treatments of the datasets  
91 with ‘control’ and ‘manipulated’ plots. LAT: latitude (WGS84 datum), and LON:  
92 longitude (WGS84 datum).

93

94 **1.** The dataset is issued from an experiment in a northern mixed prairie at a field  
95 station in Miles City, Montana, USA (LAT: 46.32, and LON: -105.80). This dataset  
96 consists of 42 plots, where each plot was sampled an average of 12.5 times. In each  
97 plot, individual plants were quantified and mapped annually. More information:  
98 <http://esapubs.org/archive/ecol/E092/143/#data>

99

100 **2.** The dataset is issued from an experiment located on a mixed grass prairie in Hays,  
101 Kansas, USA (LAT: 38.80, and LON: -99.30). This dataset consists of 51 plots, where  
102 each plot was sampled an average of 34.5 times. In each plot, individual plants were  
103 quantified and mapped. Thirty-six permanent quadrats were located inside livestock  
104 exclosures and 15 in grazed areas. More information:

105 [https://web.archive.org/web/20150128015820/http://esapubs.org:80/archive/ecol/E08](https://web.archive.org/web/20150128015820/http://esapubs.org:80/archive/ecol/E088/161/default.htm)  
106 [8/161/default.htm](https://web.archive.org/web/20150128015820/http://esapubs.org:80/archive/ecol/E088/161/default.htm)

107

108 **3.** The dataset is issued from an experiment located on a shortgrass steppe of North  
109 America in Nunn, Colorado, USA (LAT: 40.85, and LON: -104.71). This dataset  
110 consists of 24 plots, where each plot was sampled an average of 13.5 times. In each  
111 plot, individual plants were quantified and mapped. The quadrats were established in  
112 six grazed and ungrazed study sites on the Central Plains Experimental Range. There  
113 were four treatments combining past and present grazing status: ungrazed in the past  
114 and at present (ungrazed/ungrazed), grazed by livestock in the past and present  
115 (grazed/grazed), grazed in the past and ungrazed during the experiment  
116 (grazed/ungrazed), and ungrazed in the past and grazed during the experiment  
117 (ungrazed/grazed). More information:

118 [https://web.archive.org/web/20150502183659/http://www.esapubs.org/archive/ecol/E0](https://web.archive.org/web/20150502183659/http://www.esapubs.org/archive/ecol/E094/128/)  
119 [94/128/](https://web.archive.org/web/20150502183659/http://www.esapubs.org/archive/ecol/E094/128/)

120

121 **4.** The dataset is issued from an experiment located on semi-desert grasslands at the  
122 Santa Rita Experimental Range, Arizona, USA (LAT: 31.83, and LON: -110.88). This  
123 dataset consists of 160 plots, where each plot was sampled an average of 11.2 times.  
124 In each plot, individual plants were quantified and mapped. Quadrats were located in  
125 exclosures (ungrazed) and in pastures grazed by livestock (grazed). More information:  
126 [https://web.archive.org/web/20150502183207/http://esapubs.org:80/archive/ecol/E09](https://web.archive.org/web/20150502183207/http://esapubs.org:80/archive/ecol/E093/132/default.htm)  
127 [3/132/default.htm](https://web.archive.org/web/20150502183207/http://esapubs.org:80/archive/ecol/E093/132/default.htm)

128

129 **5.** The dataset is issued from an experiment located in sagebrush steppe in eastern  
130 Idaho, USA (LAT: 44.20, and LON: -112.20). This dataset consists of 23 plots, where  
131 each plot was sampled an average of 21.5 times. In each plot, individual plants were  
132 quantified and mapped. These permanent quadrats were located in both grazed (4  
133 quadrats) and ungrazed units (18 quadrats), and one quadrat was grazed in the past  
134 and ungrazed during the experiment. More information:

135 [https://web.archive.org/web/20150128015825/http://esapubs.org/archive/ecol/E091/24](https://web.archive.org/web/20150128015825/http://esapubs.org/archive/ecol/E091/243/default.htm)  
136 [3/default.htm](https://web.archive.org/web/20150128015825/http://esapubs.org/archive/ecol/E091/243/default.htm).

137

138 **6.** The dataset is issued from an experiment on the Jornada Long-Term Ecological  
139 Research site in southern New Mexico, USA (LAT: 32.83, and LON: -107.33). This  
140 dataset consists of 222 plots, where each plot was sampled an average of 8.0 times.  
141 Previously grazing domestic livestock was excluded from the area where three  
142 permanent transects (2.7 km) were established. One of the transects received  
143 fertilization of 10 g/m<sup>2</sup> of nitrogen. One of the two control transects (not fertilized),  
144 was sampled at 40 stations, the other two transects had 91 stations each. At each  
145 station abundance of each species was estimated by point-intercept method along a 30  
146 m transect perpendicular to each of the three permanent transects. More information:  
147 <https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-jrn.2100119001.50>.

148

149 **7.** The dataset is issued from an experiment on the Jornada Basin Long-Term  
150 Ecological Research Program (LTER) site in the Chihuahuan desert, New Mexico,  
151 USA (LAT: 32.93, and LON: -107.36). This dataset consists of 1001 plots, where  
152 each plot was sampled an average of 11.5 times. On the grassland site, three exclusion  
153 treatment levels were set in addition to the control treatment left open to all grazers.  
154 The first level excluded only domestic animals (cattle), the second excluded

155 lagomorphs, and the third excluded rodents. In the shrubland site, only lagomorph-  
156 and rodent-exclusion treatments were set in addition to the control. In each treatment  
157 of each site, 4 grids of 36 permanent plots (1 m<sup>2</sup>) were sampled (visual estimated  
158 cover). More information:

159 <https://portal.lternet.edu/nis/metadataviewer?packageid=knb-lter-jrn.2100086002.39>.  
160

161 **8.** The dataset is issued from an experiment in an open grassland of the South African  
162 Kalahari near Askham, South Africa (LAT: -26.76, and LON: 20.61). This dataset  
163 consists of 20 plots, where each plot was sampled an average of 10.7 times. The cover  
164 values (%) of all individual plant species were estimated annually. More information:  
165 Jürgens et al. (2010).

166

167 **9.** The dataset is issued from an experiment located in the Succulent Karoo in  
168 Soebatsfontein, South Africa (LAT: -30.19, and LON: 17.54). This dataset consists of  
169 24 plots, where each plot was sampled an average of 15.8 times. The cover values (%)  
170 of all individual plant species were estimated annually. More information: Jürgens et  
171 al. (2010).

172

173 **10.** The dataset is issued from an experiment located in the Succulent Karoo, near  
174 Leliefontein, South Africa (LAT: 18.28, and LON: -30.40). This dataset consists of 42  
175 plots, where each plot was sampled an average of 14.7 times. The cover values (%) of  
176 all individual plant species were estimated annually. More information: Jürgens et al.  
177 (2010).

178

179 **11.** The dataset is issued from an experiment located in the Succulent Karoo,  
180 Knersvlakte near Vanrhynsdorp, South Africa (LAT: -31.28, and LON: 18.59). This  
181 dataset consists of 40 plots, where each plot was sampled an average of 16.0 times.  
182 The cover values (%) of all individual plant species were estimated annually. More  
183 information: Jürgens et al. (2010).

184

185 **12.** The dataset is issued from an experiment on the Kiskun LTER located in Bugac  
186 and Orgovány sites of Kiskunság National Park, Hungary (LAT: 46.73, and LON:  
187 19.54). This dataset consists of 380 plots, where each plot was sampled an average of  
188 14.5 times. Half of the plots were fenced to control grazing pressure. In each plot, the

189 cover values (%) were visually estimated annually. More information: Kertész et al.  
190 (2017).

191

192 **13.** The dataset is issued from an experiment on a grassland in Cedar Creek LTER  
193 Ecosystem Science Reserve, Minnesota, USA (LAT: 45.41, and LON: -93.16). This  
194 dataset consists of 50 plots, where each plot was sampled an average of 7.0 times. The  
195 plots were divided in 10 treatments of fertilization and grazing exclusion (Control=no  
196 treatment, K=potassium, P=phosphate, N=nitrogen, PK=phosphate and potassium,  
197 NK=nitrogen and potassium, NP=nitrogen and phosphate, NPK=nitrogen, phosphate  
198 and potassium, Fence=Fence, NPK+Fence=nitrogen, phosphate and potassium +  
199 fence). In each plot, the cover values (%) were visually estimated annually. This  
200 dataset was provided from Cedar Creek LTER. More information:

201 <http://cedarcreek.umn.edu/research/data/dataset?acze247>.

202

203 **14.** The dataset is issued from an experiment located in the Cedar Creek LTER  
204 Ecosystem Science Reserve, Minnesota, USA (LAT: 45.41, and LON: -93.19). This  
205 dataset consists of 184 plots, where each plot was sampled an average of 6.2 times.  
206 Plots were distributed across 6 treatments with increasing burning frequency: i) no  
207 burning – control – (48 plots), ii) 1 per 10 years (16 plots), iii) 1 per 3 years (32 plots),  
208 iv) 1 per 2 years (32 plots), v) 2 per 3 years (8 plots) and vi) 4 per 5 years (48 plots).  
209 Plots are located on 12 management areas ranging in size from 2.4 to 30 ha. In each  
210 plot, the cover values (%) were visually estimated. More information:

211 <http://cedarcreek.umn.edu/research/data/dataset?herbe133>.

212

213 **15.** The dataset is issued from an experiment located in the Cedar Creek LTER  
214 Ecosystem Science Reserve, Minnesota, USA (LAT: 45.41, and LON: -93.19). This  
215 dataset consists of 60 plots, where each plot was sampled an average of 24.8 times. In  
216 each plot, the biomass of individual plants was recorded from 4 plots (0.3 m<sup>2</sup>) per  
217 field until 2013. More information:

218 <http://cedarcreek.umn.edu/research/data/dataset?ple054>.

219

220 **16.** The dataset is issued from an experiment located in the Cedar Creek LTER  
221 Ecosystem Science Reserve, Minnesota, USA (LAT: 45.40, and LON: -93.20). This  
222 dataset consists of 234 plots, where each plot was sampled an average of 22.0 times.

223 The experiment combines different levels of fertilization on 4 fields that were  
224 abandoned for different periods (14, 25, 48 years and never ploughed before the  
225 experiment started in 1982) and where mammal grazers were excluded. In each plot,  
226 individual plant biomass was recorded on 5 to 6 replicate plots of different  
227 fertilization treatments (from 0 to 40 g/m<sup>2</sup> of nitrogen) per field every year. More  
228 information: <http://cedarcreek.umn.edu/research/data/dataset?ple001>.

229

230 **17.** The dataset is issued from an experiment located in the Cedar Creek LTER  
231 Ecosystem Science Reserve, Minnesota, USA (LAT: 45.40, and LON: -93.20). This  
232 dataset consists of 237 plots, where each plot was sampled an average of 14.8 times.  
233 The experiment combines 9 levels of fertilization (from 0 to 40 g/m<sup>2</sup> of nitrogen) and  
234 prescribed burning on three fields that were abandoned since 14, 25 and 48 years, and  
235 where mammal grazers were excluded. All 3 fields had 6 replicate plots of the 9  
236 fertility treatments from 1982. From 1992 half of the plots in field B were burned  
237 every spring, and half of the plots in field A and C stopped receiving the fertilization  
238 treatment. To maintain continuity of the treatments within plots the 1992-2011 period  
239 of those plots were entered in the database as separate plots of the same data set.  
240 Individual plant biomass was measured. More information:  
241 <http://cedarcreek.umn.edu/research/data/dataset?ple002>.

242

243 **18.** The dataset is issued from an experiment located in the Shortgrass Steppe LTER  
244 in the Central Plains Experimental Range, Colorado, USA (LAT: 40.85, and LON: -  
245 104.77). This dataset consists of 795 plots, where each plot was sampled an average  
246 of 13.5 times. Plots were distributed across four combinations of past/current  
247 management: grazed/grazed, ungrazed/ungrazed, grazed/ungrazed and  
248 ungrazed/grazed. In 1998, additional plots were added in a fifth treatment with fences  
249 excluding both large and small grazers (rodent exclusion). More information:  
250 <https://portal.lternet.edu/nis/metadataviewer?packageid=knb-lter-sgs.527.1>.

251

252 **19.** The dataset is issued from an experiment located in sandy semi-natural grasslands  
253 of the Elbe valley in H6hbeck, Germany (LAT: 53.05, and LON: 11.41). This dataset  
254 consists of 96 plots, where each plot was sampled an average of 6.0 times. The  
255 vegetation was surveyed once a year in 1 m<sup>2</sup> plots using the Londo scale (Londo  
256 1976). More information: Schuhmacher & Dengler (2013).

257

258 **20.** The dataset is issued from an experiment located near Dufftown, Morayshire,  
259 United Kingdom (LAT: 57.73, and LON: -3.10). This dataset consists of 12 plots,  
260 where each plot was sampled an average of 6.0 times. Each species was measured in a  
261 transect, using the inclined-point quadrat method (Tinney et al. 1937) ( $32.5^\circ$  to the  
262 horizontal). All contacts with 5 pins were recorded in 20 quadrat positions per plot.  
263 More information: Pakeman et al. (2003).

264

265 **21.** The dataset is issued from an experiment located in Andrew Experimental forest  
266 Program (AND-LTER), Oregon, USA (LAT: 44.35, and LON: -122.41). This dataset  
267 consists of 193 plots, where each plot was sampled an average of 21.4 times. Plots  
268 were established in i) undisturbed, ii) logged, iii) logged and lightly burned, and iv)  
269 logged and severely burned areas. In each plot, the cover values (%) were estimated.  
270 More information: [https://portal.lternet.edu/nis/metadataviewer?packageid=knb-lter-](https://portal.lternet.edu/nis/metadataviewer?packageid=knb-lter-and.3217.11)  
271 [and.3217.11](https://portal.lternet.edu/nis/metadataviewer?packageid=knb-lter-and.3217.11).

272

273 **22.** The dataset is issued from an experiment located on woodlands, grasslands, and  
274 shrublands in eastern Australia (LAT: -30.12, and LON: 147.17). This dataset consists  
275 of 47 plots, where each plot was sampled an average of 10.2 times. In each plot, the  
276 biomass of the vegetation was measured annually, from 1991 to 2002, in four 300 m  
277 long transects each containing 13 quadrats of 0.72 m x 0.72 m. Dataset owners: James  
278 Val and David Eldridge (Office of Environment & Heritage, University of New South  
279 Wales).

280

281 **23.** The dataset is issued from an experiment located on a pasture in Fasque, United  
282 Kingdom (LAT: 56.87, and LON: -2.60). This dataset consists of eight plots, where  
283 each plot was sampled an average of 8.0 times. Inclined-point quadrat method ( $32.5^\circ$   
284 to the horizontal) was used to record each species in a transect, with a minimum of 20  
285 point contacts at 18 locations per plot (i.e. a minimum of 360 contacts per plot). More  
286 information: Marriott et al. (2002).

287

288 **24.** The dataset is issued from an experiment located on La Fage French National  
289 Institute for Agricultural Research (INRA) experimental station, close to Millau,  
290 France (LAT: 43.92, and LON: 3.10). This dataset consists of 16 plots, where each

291 plot was sampled an average of 28.0 times. Individual plants were identified using the  
292 point intercept method on 5 m permanent lines (1 point/10 cm, i.e. 50 points/line).  
293 More information: Chollet et al. (2014) and Garnier et al. (2018).

294

295 **25.** The data sourced from BioTIME (Dornelas et al. 2018), Study\_ID 483 and 497-  
296 ITEX Dataset 5 - Teberda (Malaya Alpine-Snowbed and Geranium Hedysarum  
297 Meadow) and ITEX Dataset 19 - Teberda (Festuca Varia Grassland, Malaya Alpine  
298 Lichen-Heath). The dataset is issued from an experiment located in Teberda State  
299 Reserve, a part of the Karachaevo-Cherkessian Republic in the northwestern  
300 Caucasus, Russia (LAT: 43.45, and LON: 41.69). This dataset consists of 145 plots,  
301 where each plot was sampled an average of 24.3 times. In each plot, the cover of each  
302 plant species was recorded as number of shoots per m<sup>2</sup>. More information:  
303 Onipchenko *et al.* (1998).

304

305 **26.** The dataset is issued from an experiment located a moorland in the Clocaenog  
306 Forest, United Kingdom (LAT: 53.06, and LON: -3.47). This dataset consists of 9  
307 plots, where each plot was sampled an average of 12.0 times. The experiment was  
308 designed with three treatments: control, drought (~20% reduction in total annual  
309 rainfall) and warming (~64% reduction in heat loss during night and 14% reduction in  
310 total annual rainfall). Three quadrats per plot were chosen, and in each quadrat  
311 vegetation was quantified using a grid of 100 pins (pin-point methodology). Pin hits  
312 were then converted to biomass (g m<sup>-2</sup>) using a biomass calibration-conversion. More  
313 information: [https://catalogue.ceh.ac.uk/documents/5b39a644-d614-4f2b-8df6-](https://catalogue.ceh.ac.uk/documents/5b39a644-d614-4f2b-8df6-202ed440b4ab)  
314 [202ed440b4ab](https://catalogue.ceh.ac.uk/documents/5b39a644-d614-4f2b-8df6-202ed440b4ab). Doi: [https://doi.org/10.5285/5b39a644-d614-4f2b-8df6-](https://doi.org/10.5285/5b39a644-d614-4f2b-8df6-202ed440b4ab)  
315 [202ed440b4ab](https://doi.org/10.5285/5b39a644-d614-4f2b-8df6-202ed440b4ab).

316

317 **27.** The dataset is issued from an experiment located on serpentine and non-serpentine  
318 meadows in California, USA (LAT: 38.85, and LON: -123.50). This dataset consists  
319 of 400 plots, where each plot was sampled an average of 10.0 times. In each plot, the  
320 species cover (%) was visually estimated annually. More information: Fernandez-  
321 Going et al. (2012) and Harrison (1999).

322

323 **28.** The dataset is issued from an experiment located on the Jornada Basin  
324 Experimental Range JRN-LTER in the Chihuahuan desert, New Mexico, USA (LAT:

325 32.62, and LON: -106.67). This dataset consists of 68 plots, where each plot was  
326 sampled an average of 27.8 times. Density of individuals per species and per plot was  
327 recorded. More information:

328 <https://portal.lternet.edu/nis/metadataviewer?packageid=knb-lter-jrn.210351002.75>.

329

330 **29.** The dataset is issued from an experiment located on a grassland in Krkonose  
331 Mountains, Czech Republic (LAT: 50.69, and LON: 15.71). This dataset consists of  
332 four plots, where each plot was sampled an average of 16.8 times. Standing biomass  
333 was sampled annually. More information: Herben et al. (1997).

334

335 **30.** The dataset is issued from an experiment located on a grassland in Krkonose  
336 Mountains, Czech Republic (LAT: 50.69, and LON: 15.79). This dataset consists of  
337 four plots, where each plot was sampled an average of 29.8 times. Standing biomass  
338 was sampled annually. More information: Herben et al. (2017).

339

340 **31.** The data sourced from BioTIME (Dornelas et al. 2018), Study\_ID 243 - Virginia  
341 Coast Reserve Long-Term Ecological Research. The dataset is issued from an  
342 experiment located in the coastal sand dunes of Hog island, Virginia, USA (LAT:  
343 37.67, and LON: -75.67). This dataset consists of 28 plots, where each plot was  
344 sampled an average of 18.9 times. Half of the plots received nitrogen fertilization each  
345 year in the form of urea nitrogen (30% uncoated (46-0-0) and 70% (40-0-0) coated for  
346 slow release). The fertilizer was applied evenly in a dry form (15 g/m<sup>2</sup> of nitrogen). In  
347 each plot, species cover (%) was visually estimated in five 0.25 m<sup>2</sup> plots. More  
348 information: Day et al. (2016).

349

350 **32.** The dataset is issued from an experiment located on a grassland near Napal, Spain  
351 (LAT: 42.72, and LON: -1.22). This dataset consists of 12 plots, where each plot was  
352 sampled an average of 12.0 times. The experimental area was fenced and shrubs were  
353 removed. Six plots were fertilized (sewage sludge to the soil surface with 5000 g/m<sup>2</sup>)  
354 and six plots were used as controls. All vascular plant species were measured annually  
355 using frequencies. To do so, each plot was divided into 100 subplots, and the  
356 presence/absence of each species was recorded. More information: Gazol et al.  
357 (2016).

358

359 **33.** The data were sourced from BioTIME (Dornelas et al. 2018), Study\_ID 491 -  
360 ITEX Dataset 13 - Toolik (Dry, Moist). The dataset is issued from an experiment  
361 located on tundra vegetation near Toolik, Alaska, USA (LAT: 68.62, and LON: -  
362 149.61). This dataset consists of eight plots, where each plot was sampled an average  
363 of 6.0 times. The plots are divided between dry tundra with control and warming  
364 treatments and moist tundra with only control treatment. Biomass estimates were  
365 obtained using a fixed 75 cm<sup>2</sup> point frame, with 100 measurements spaced 7 cm apart.  
366

367 **34.** The data was sourced from BioTIME (Dornelas et al. 2018), Study\_ID 492 -  
368 ITEX Dataset 14 - Toolik (LTER Heath, LTER Moist acidic tussock, LTER non-  
369 acidic tussock, LTER wet sedge, SAG wet sedge2, Tussock 1981 plots). The dataset  
370 is issued from an experiment located in Toolik, Alaska, USA (LAT: 68.63, and LON:  
371 -149.58). This dataset consists of four plots, where each plot was sampled an average  
372 of 6.0 times. In each plot, species biomass was assessed by clipping of four or five  
373 0.25 m x 0.25 m plots, and sorting to species level.  
374

375 **35.** The dataset is issued from an experiment located on a grassland in Bayreuth,  
376 Germany (LAT: 49.92, and LON: 11.59). This dataset consists of 15 plots, where  
377 each plot was sampled an average of 7.7 times. Three treatments were applied: 1)  
378 control (ambient condition), 2) winter warming (October–March), and 3) summer  
379 warming (April–September). In each plot, species cover (%) was visually estimated  
380 annually. More information: Grant et al. (2017).  
381

382 **36.** The dataset is issued from an experiment located on a grassland in the Czech  
383 Republic (LAT: 48.87, and LON: 16.64). This dataset consists of seven plots, where  
384 each plot was sampled an average of 8.0 times. In each plot (1 m<sup>2</sup>), the species cover  
385 (%) was visually estimated annually from 1993 to 2001. Dataset owner: Jiří Danihelka  
386 (Department of Botany and Zoology, Masaryk University and Department of  
387 Vegetation Ecology, Institute of Botany, The Czech Academy of Sciences).  
388

389 **37.** The dataset is issued from an experiment located on a grassland in Laqueuille,  
390 France (LAT: 45.64, and LON: 2.73). This dataset consists of 10 plots, where each  
391 plot was sampled an average of 13.0 times. Half of the plots were located in an  
392 intensively managed grassland (10-15 animals ha<sup>-1</sup> yr<sup>-1</sup> and 20 g/m<sup>2</sup> of nitrogen), and

393 the other half were located in a neighbouring grassland under extensive management  
394 (5-8 animals ha<sup>-1</sup> yr<sup>-1</sup> and no fertilization). In each plot, presence/absence of each  
395 species was recorded in 40 pin-points regularly spaced (pin-point methodology.  
396 Dataset owner: Katja Klumpp (INRA, Grassland Ecosystem Research Unit).

397

398 **38.** The dataset is issued from an experiment located on Shortgrass Steppe (SGS-  
399 LTER) in the Central Plains Experimental Range Nunn, Colorado, USA (LAT: 40.85,  
400 and LON: -104.71). This dataset consists of 48 plots, where each plot was sampled an  
401 average of 9.0 times. The experiment evaluated four treatments: control inside  
402 enclosure, control outside enclosures, *Bouteloua gracilis* removal inside enclosure and  
403 *Bouteloua gracilis* removal outside enclosure. Species density was measured in a  
404 quadrat (1 m<sup>2</sup>) using vegetation point intercept method (40 points of contact was  
405 recorded for each quadrat). More information:

406 <https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-sgs.703.1>.

407

408 **39.** The dataset is issued from an experiment located on a wet meadow in Ohrazeni,  
409 Czech Republic (LAT: 48.95, and LON: 14.59). This dataset consists of 12 plots,  
410 where each plot was sampled an average of 16.0 times. The experiment evaluated four  
411 treatments: control, mowing (annually in the second half of June), fertilization (65  
412 g/m<sup>2</sup> of commercial NPK fertilizer) and dominant removal (*Molinia caerulea* plants  
413 were manually removed annually). In each plot, the biomass of each species was  
414 measured annually. More information: Lepš (2014).

415

416 **40.** The dataset is issued from an experiment (Long Term Experiment SOERE-  
417 ACBB) located on a grassland in Theix, France (LAT: 45.72, and LON: 3.02). This  
418 dataset consists of eight plots, where each plot was sampled an average of 8.0 times.  
419 The experiment evaluated, on one hand, the effect of the intensity of grazing with two  
420 treatments with cattle rotational grazing at high (Ca+) or low (Ca-) level of herbage  
421 utilisation; these two treatments did not receive any mineral fertilisation. On the other  
422 hand, it also evaluated the effect of nutrient availability, comparing two treatments  
423 conducted under fixed cutting regime (three cuts/per year), one with fertilization  
424 (NPK fertilizer) and the other without fertilization. The presence/absence of each  
425 plant species was measured using 40 pin-points regularly spaced along fixed transects.  
426 Complementarily, at each pin-point, 6 points are distributed to species according to

427 visual estimation of their volume. Dataset owner: Frédérique Louault (INRA-UREP).  
428 More information: Louault et al. (2017).

429

430 **41.** The dataset is issued from an experiment belonging to the Sevilleta LTER and  
431 located on Chihuahuan desert in Sevilleta National Wildlife Refuge, New Mexico,  
432 USA (LAT: 34.27, and LON: -106.68). This dataset consists of six plots, where each  
433 plot was sampled an average of 14.3 times. More information:

434 <https://portal.itsernet.edu/nis/mapbrowse?packageid=knb-lter-sev.200.174699>.

435

436 **42.** The dataset is issued from an experiment located on hyper-oceanic coastal  
437 grasslands in United Kingdom (LAT: 57.27, and LON: -7.40). This dataset consists of  
438 48 plots, where each plot was sampled an average of 6.8 times. The experiment  
439 evaluated six treatments: 1) vertebrate grazing exclusion, 2) burial box with no sand  
440 added, 3) buried to 10 cm, 4) buried to 20 cm, 5) windbreak - shelter from prevailing  
441 SW winds, 6) no treatment. The cover values (%) of all individual plant species were  
442 estimated annually from 2004 to 2010. Data owners: Robin Pakeman (James Hutton  
443 Institute, Aberdeen) and Jack J. Lennon (School of Biological Sciences, Queen's  
444 University Belfast).

445

446 **43.** The dataset is issued from an experiment located on a grassland in Cleish and  
447 Kirkton, United Kingdom (LAT: 56.29, and LON: -4.07). This dataset consists of 16  
448 plots, where each plot was sampled an average of 6.0 times. The experiment evaluated  
449 ungrazed and sheep-grazed plots to maintain three different levels of sward height. In  
450 each plot, the inclined-point quadrat method ( $32.5^\circ$  to the horizontal) at 20 locations  
451 (with a minimum of 25 contacts per location) was used to measure each species. More  
452 information: Hulme et al. (1999).

453

454 **44.** The dataset is issued from an experiment located on a grassland in Bell Hill and  
455 Cleish, United Kingdom (LAT: 55.80, and LON: -2.84). This dataset consists of eight  
456 plots, where each plot was sampled an average of 7.0 times. In each plot, the inclined-  
457 point quadrat method ( $32.5^\circ$  to the horizontal) at 20 locations (with a minimum of 25  
458 contacts per location) was used to measure each species. More information: Grant et  
459 al. (1996a).

460

461 **45.** The dataset is issued from an experiment located on a grassland in Cleish and  
462 Sourhope, United Kingdom (LAT: 55.81, and LON: -2.86). This dataset consists of  
463 seven plots, where each plot was sampled an average of 6.0 times. There were  
464 different treatments where cattle or sheep density was adjusted twice a week to  
465 maintain the vegetation height between tussocks. In each plot, the inclined-point  
466 quadrat method ( $32.5^\circ$  to the horizontal) at 20 locations (with a minimum of 25  
467 contacts per location) was used to measure each species. More information: Grant et  
468 al. (1996) and Common et al. (1998).

469

470 **46.** The dataset is issued from an experiment located on a moorland previously on the  
471 Burnhead heft at the Redesdale Experimental Farm in Northumberland, United  
472 Kingdom (LAT: 55.37, and LON: -2.45). This dataset consists of 12 plots, where each  
473 plot was sampled an average of 6.0 times. The 12 plots were divided in three areas  
474 with different grazing treatments: ungrazed, sheep-grazed (three levels: 0.4, 0.8 and  
475  $1.2 \text{ ha}^{-1} \text{ yr}^{-1}$ ). In each plot, the inclined-point quadrat method ( $32.5^\circ$  to the horizontal)  
476 at 20 locations (with a minimum of 25 contacts per location) was used to measure  
477 each species. More information: Pakeman & Nolan (2009).

478

479 **47.** The dataset is issued from an experiment located on a heather moorland at  
480 Dundonnell near Ullapool and at Claonaig, near Tarbert Loch Fyne, Argyll and Bute,  
481 United Kingdom (LAT: 57.35, and LON: -5.55). This dataset consists of 17 plots,  
482 where each plot was sampled an average of 6.0 times. The experiment had different  
483 sheep grazing and exclusion treatments: 1) low at  $0.4 \text{ sheep ha}^{-1} \text{ yr}^{-1}$ , 2) moderate at  
484  $0.8 \text{ sheep ha}^{-1} \text{ yr}^{-1}$ , 3) high at  $1.2 \text{ sheep ha}^{-1} \text{ yr}^{-1}$ , 4) fenced against both cattle and  
485 sheep, and 5) fenced against cattle, also 6) sheep and cattle recorded from the open  
486 hill. In each plot, the inclined-point quadrat method ( $32.5^\circ$  to the horizontal) at 20  
487 locations was used to measure each species. More information: Pakeman & Nolan  
488 (2009).

489

490 **48.** The dataset is issued from an experiment located on a grassland in the Ordesa-  
491 Monte Perdido National Park, Spain (LAT: 42.67, and LON: -0.06). This dataset  
492 consists of four plots, where each plot was sampled an average of 19.0 times. The  
493 point intercept method at 20 locations was used to measure each species.

494 In each plot, the point intercept method was used annually to measure vegetation  
495 along two perpendicular transects (a total of 400 sample points). More information:  
496 Pardo et al. (2015).

497

498 **49.** The dataset is issued from an experiment located in Soto de Viñuelas, Spain  
499 (LAT: 40.60, and LON: -3.63). This dataset consists of 68 plots, where each plot was  
500 sampled an average of 11.5 times. In each plot, all plant species was recorded using  
501 presence/absence data in five quadrats of 400 cm<sup>2</sup> each from 1980 to 1995. Dataset  
502 owner: Begoña Peco (Ecology Department Autonomous, University of Madrid).

503

504 **50.** The dataset is issued from an experiment located on a shrubland in Garraf, Spain  
505 (LAT: 41.30, and LON: 1.82). This dataset consists of nine plots, where each plot was  
506 sampled an average of 17.0 times. Three experiment evaluated three treatments: 1)  
507 control, 2) warming (metallic curtain covering the plots during the night), and 3)  
508 drought (transparent curtain covering the plots during rainfall). Number of contacts  
509 per plot was used to quantify each species. Dataset owners: Josep Penuelas, Marc  
510 Estiarte and Romà Ogaya (Global Ecology Unit CREA-CSIC-UAB).

511

512 **51.** The dataset is issued from an experiment belong to the Jornada LTER (JRN-  
513 LTER) and located in Chihuahuan desert, Jornada Basin Experimental Range, New  
514 Mexico, USA (LAT: 32.00, and LON: -106.00). This dataset consists of 734 plots,  
515 where each plot was sampled an average of 24.0 times. In each plot, the biomass of  
516 each species was calculated from field measurement of individual species cover and  
517 height. More information:

518 <https://portal.lternet.edu/nis/metadataviewer?packageid=knb-lter-jrn.2100011001.49>.

519

520 **52.** The dataset is issued from an experiment located on a moorland on the Burnhead  
521 heft at the Redesdale Experimental Farm in Northumberland, United Kingdom (LAT:  
522 55.37, and LON: -2.45). This dataset consists of 10 plots, where each plot was  
523 sampled an average of 6.0 times. The experiment had different grazing treatments:  
524 summer grazing, winter grazing or year-round grazing (0.7 sheep ha<sup>-1</sup> yr<sup>-1</sup>), year-  
525 round grazing (1.4 sheep ha<sup>-1</sup> yr<sup>-1</sup>), and no grazing. In each plot, the inclined-point  
526 quadrat method (32.5° to the horizontal) at 20 locations (with a minimum of 25

527 contacts per location) was used to measure each species. More information: Hulme et  
528 al. (2002) and Pakeman & Nolan (2009).

529

530 **53.** The dataset is issued from an experiment located on moorlands in Derbyshire,  
531 United Kingdom (LAT: 54.69, and LON: -2.41). This dataset consists of 216 plots,  
532 where each plot was sampled an average of 10.0 times. The experiment evaluated 36  
533 treatments: no treatment; cut once per year; cut twice per year; herbicide sprayed;  
534 herbicide sprayed in first year, cut in second; and cut in first year, sprayed in second.  
535 Within each of these main plot treatments there were two sub-plot grazing treatments  
536 - sheep grazing and no sheep grazing. Finally, there were three restoration treatments  
537 applied at the sub-sub-plot level: untreated, *Calluna* moorland litter applied as litter,  
538 and *Calluna* vegetation applied as cut brush. All these 36 treatments had 6 replicates.  
539 In each plot, the species composition was recorded using point-quadrats (1 m-long  
540 frame with 10 pin positions at 10 cm intervals, pin diameter = 2 mm). Dataset owner:  
541 Rob Marrs (University of Liverpool).

542

543 **54.** The dataset is issued from an experiment belonging to the Environmental Change  
544 Network (ECN) and located in the United Kingdom (LAT: 53.95, and LON: -3.23).  
545 This dataset consists of 198 plots, where each plot was sampled an average of 11.1  
546 times. In each plot (ten quadrats of 0.16 m<sup>2</sup>), the inclined-point quadrat method was  
547 used to evaluate the vegetation annually. More information: Rennie et al. (2016) and  
548 <https://catalogue.ceh.ac.uk/documents/b98efec8-6de0-4e0c-85dc-fe4cdf01f086> and  
549 <https://catalogue.ceh.ac.uk/documents/d349babc-329a-4d6e-9eca-92e630e1be3f>.

550

551 **55.** The dataset is issued from an experiment belonging to the Andrews Forest LTER  
552 (AND-LTER) and located in a forest in the Oregon Cascade Range, USA (LAT:  
553 44.22, and LON: -122.25). This dataset consists of 5 plots, where each plot was  
554 sampled an average of 10.0 times. The vegetation cover (%) was visually estimated 10  
555 times in a quadrat of 4 m<sup>2</sup> for trees (vegetation > 60 cm tall) and 9 quadrats (0.1 m<sup>2</sup>)  
556 for herb and low shrub (< 60 cm tall). More information: Rothacher (Rothacher 2013)  
557 and <https://portal.lter.net.edu/nis/mapbrowse?packageid=knb-lter-and.3190.7>.

558

559 **56.** The dataset is issued from an experiment belonging to the Park Grass permanent  
560 grassland and located in Rothamsted, United Kingdom (LAT: 51.81, and LON: -

561 0.37). This dataset consists of 74 plots, where each plot was sampled an average of  
562 9.9 times. The purpose of the experiment was to evaluate different fertility and lime  
563 treatments. Herbage was taken from six randomly located quadrats measuring 0.5 m x  
564 0.25 m within each plot, resulting in a total sampling area of 0.75 m<sup>2</sup> within each plot.  
565 In each plot, the biomass of each species was measured annually in quadrats  
566 (sampling area: 0.75 m<sup>2</sup>). More information: Crawley et al. (2005) and  
567 <http://www.era.rothamsted.ac.uk/Park>.

568

569 **57.** The dataset is issued from an experiment located on a savannah in central Spain  
570 (LAT: 40.38, and LON: -4.20). This dataset consists of 210 plots, where each plot was  
571 sampled an average of 6.0 times. The experiment evaluated two types of pastures  
572 (higher-productivity pastures and low-productivity pastures) and three treatments  
573 (ungrazed, grazed by small herbivores, and grazed by large and small herbivores). In  
574 each plot, the species cover (%) was visually estimated. More information: Rueda et  
575 al. (2013).

576

577 **58.** The dataset is issued from an experiment located in Central Germany (LAT:  
578 51.55, and LON: 10.07). This dataset consists of 14 plots, where each plot was  
579 sampled an average of 14.9 times. In each plot, species vegetation cover (%) was  
580 visually estimated. More information: Schmidt (2007).

581

582 **59.** The dataset is issued from an experiment located on a former arable field in the  
583 Experimental Botanical Garden of the University of Göttingen, Germany (LAT:  
584 51.56, and LON: 9.96). This dataset consists of six plots, where each plot was  
585 sampled an average of 38.0 times. In each plot, species vegetation cover (%) was  
586 visually estimated. More information: Schmidt (Schmidt 2006) and Bernhardt-  
587 Römermann et al. (2011).

588

589 **60.** The dataset is issued from an experiment located in the Swiss National Park  
590 (IUCN Ia reserve, LAT: 46.68, and LON: 10.22). This dataset consists of 41 plots,  
591 where each plot was sampled an average of 12.2 times. In each plot, plant species  
592 cover (%) was visually estimated. More information: Braun-Blanquet et al. (1931),  
593 Schütz et al. (2000).

594

595 **61.** The dataset is issued from an experiment belonging to the Sevilleta LTER (SEV-  
596 LTER) and located in Sevilleta National Wildlife Refuge, New Mexico, USA (LAT:  
597 34.31, and LON: -106.49). This dataset consists of 95 plots, where each plot was  
598 sampled an average of 9.8 times. The experiment was designed to evaluate the effect  
599 of prescribed burning (two areas were left unburned as control treatments, and the  
600 other plots were burned in different dates) and grazing exclusion (fenced and  
601 unfenced). In each plot, the individuals present in 36 quadrats (0.1 m<sup>2</sup>) were recorded.  
602 More information: <https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-sev.148.131885>.

604

605 **62.** The dataset is issued from an experiment belonging to the Sevilleta LTER (SEV-  
606 LTER) and located in Sevilleta National Wildlife Refuge, New Mexico, USA (LAT:  
607 34.33, and LON: -106.74). This dataset consists of 81 plots, where each plot was  
608 sampled an average of 9.2 times. The experiment had three treatments: 1) control  
609 plots (natural rainfall regime) 2) drought was induced by rainfall shelters, and 3)  
610 watering was applied by redirecting the water from the nearby rainfall shelters. In  
611 each plot, the plant cover (%) was estimated every spring. More information:  
612 <https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-sev.147.167839>.

613

614 **63.** The dataset is issued from an experiment belonging to the Sevilleta LTER (SEV-  
615 LTER) and located on a grassland in Sevilleta National Wildlife Refuge, New  
616 Mexico, USA (LAT: 34.33, and LON: -106.63). This dataset consists of 216 plots,  
617 where each plot was sampled an average of 7.7 times. The experiment evaluated the  
618 impact of prairie dog reintroduction (grazed and ungrazed areas) on vegetation. In  
619 each plot, the plant cover (%) was estimated annually. More information:  
620 <https://portal.lternet.edu/nis/metadataviewer?packageid=knb-lter-sev.212.4>.

621

622 **64.** The dataset is issued from an experiment belonging to the Sevilleta LTER (SEV-  
623 LTER) and located on a woodland in Sevilleta National Wildlife Refuge, New  
624 Mexico, USA (LAT: 34.37, and LON: -106.54). This dataset consists of 100 plots,  
625 where each plot was sampled an average of 13.0 times. In each plot, the plant cover  
626 (%) was visually estimated annually. More information:  
627 <https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-sev.278.245672>.

628

629 **65.** The dataset is issued from an experiment belonging to the Sevilleta LTER (SEV-  
630 LTER) and located in Sevilleta National Wildlife Refuge, New Mexico, USA (LAT:  
631 34.37, and LON: -106.58). This dataset consists of 100 plots, where each plot was  
632 sampled an average of 16.4 times. The experiment evaluated three treatments: 1)  
633 control plots (untouched vegetation), 2) removal of all three dominant species (*Larrea*  
634 *tridentata*, *Bouteloua eriopoda*, *Bouteloua gracilis*), and 3) removal of one dominant  
635 species. In each plot, the plant cover (%) was visually estimated annually. More  
636 information: [https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-](https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-sev.168.192543)  
637 [sev.168.192543](https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-sev.168.192543).  
638

639 **66.** The dataset is issued from an experiment belonging to the Shortgrass Steppe  
640 LTER (SGS-LTER) and located on grasslands and shrublands in Central Plains  
641 Experimental Range, Colorado, USA (LAT: 40.85, and LON: -104.77). This dataset  
642 consists of 18 plots, where each plot was sampled an average of 8.2 times. In each  
643 plot, the plant cover was recorded on three permanent transects (1 m<sup>2</sup>: sum of plots  
644 along the transect). More information: Stapp (Stapp 2013) and  
645 <https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-sgs.140.17>.  
646

647 **67.** The dataset is issued from an experiment located in a beech forest near Göttingen,  
648 Central Germany (LAT: 51.57, and LON: 10.32). This dataset consists of seven plots,  
649 where each plot was sampled an average of 18.0 times. Four plots had a fertilization  
650 treatment (NP addition) and three were the control plots. In each plot, the species  
651 cover (%) was visually estimated. More information: Schmidt (2009).  
652

653 **68.** The dataset is issued from an experiment located on a meadow near Zvíkov,  
654 Czech Republic (LAT: 48.99, and LON: 14.61). This dataset consists of 40 plots,  
655 where each plot was sampled an average of 10.3 times. The experiment evaluated four  
656 treatments: 1) control (intact vegetation), 2) mycorrhizal grasses and forbs left, non-  
657 mycorrhizal species weeded out, 3) mycorrhizal forbs remaining, everything else  
658 weeded out, and 4) mycorrhizal grasses remaining, everything else weeded out. In  
659 each plot, the species cover (%) was visually estimated annually. More information:  
660 Šmilauer & Šmilauerová (2013).  
661

662 **69.** The dataset is issued from an experiment located on a floodplain grassland in  
663 Anloo and Taarlo, The Netherlands (LAT: 53.05, and LON: 6.66). This dataset  
664 consists of 80 plots, where each plot was sampled an average of 28.9 times. In each  
665 plot, the species cover (%) was estimated almost every year from 1973 to 2008.  
666 Dataset owners: Christian Smit and Jan P. Bakker (Conservation Ecology Group,  
667 Groningen Institute for Evolutionary Life Sciences).

668

669 **70.** The dataset is issued from an experiment located on a meadow in the north-eastern  
670 Tibetan Plateau in Qinghai Province, China (LAT: 37.62, and LON: 101.20). This  
671 dataset consists of 30 plots, where each plot was sampled an average of 9.0 times. The  
672 experiment was designed to evaluate 10 nitrogen treatments (no N added and 9  
673 combinations of three N forms and three N rates). In each plot, the species cover (%)  
674 was visually estimated annually. More information: Song et al. (2012).

675

676 **71.** The dataset is issued from an experiment located on salt marshes of the  
677 Schleswig-Holstein Wadden Sea National Park in Hamburger Hallig and  
678 Westerhever, Germany (LAT: 54.49, and LON: 8.75). This dataset consists of 212  
679 plots, where each plot was sampled an average of 18.7 times. There were two  
680 treatments in Westerhever: natural condition and intensive grazing, and only natural  
681 conditions in Hamburger Hallig. In each plot, the species cover was measured  
682 annually using the Londo scale (percentage of vegetation cover) from 1997 to 2015 in  
683 Hamburger Hallig and from 1995 to 2012 in Westerhever. Dataset owner: Martin  
684 Stock (Wadden Sea National Park of Schleswig-Holstein).

685

686 **72.** The dataset is issued from an experiment located on a wooded savanna in  
687 Laikipia, Kenya (LAT: 0.28, and LON: 36.87). This dataset consists of 18 plots,  
688 where each plot was sampled an average of 14.7 times. The treatments were six  
689 combinations (3 replicates) of cattle, wildlife, and mega-herbivore grazing. These  
690 either allowed (1) the entry of all large mammalian herbivores, (2) all large  
691 mammalian herbivores except mega-herbivores (elephants *Loxodonta africana* and  
692 giraffe *Giraffa camelopardis*) to enter, or (3) excluded all large herbivores. In each  
693 plot, vegetation was assessed annually by counting the number of pins hit by each  
694 species over a ten-point pin frame at each station. More information: Veblen et al.  
695 (2016).

696

697 **73.** The dataset is issued from an experiment located on a coastal heathland in  
698 Lurekalven, Norway (LAT: 60.70, and LON: 5.08). This dataset consists of 42 plots,  
699 where each plot was sampled an average of 6.0 times. In each plot, all vascular plants,  
700 bryophytes and lichens were recorded annually using frequencies (1 m x 1 m metal  
701 frame divided into 16 subplots). More information: Vandvik et al. (2005).

702

703 **74.** The dataset is issued from an experiment located in Bonanza Creek LTER,  
704 Alaska, USA (LAT: 65.00, and LON: -148.00). This dataset consists of 59 plots,  
705 where each plot was sampled an average of 12.0 times. In each plot, the species cover  
706 (%) was visually estimated. More information: Viereck et al. (2010) and  
707 <https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-bnz.174.19>.

708

709 **75.** The dataset is issued from an experiment located on desert steppes in Gobi Gurvan  
710 Saykhan National Park, Mongolia (LAT: 43.61, and LON: 104.13). This dataset  
711 consists of 18 plots, where each plot was sampled an average of 7.1 times. The  
712 experiment evaluated two treatments: 1) exclusion of large ungulates, and 2) no  
713 exclusion of large ungulates. In each plot, the species cover (%) was visually  
714 estimated annually. More information: Wesche et al. (2010).

715

716 **76.** The dataset is issued from an experiment located on a floodplain grassland on  
717 formerly arable land (LAT: 51.78, and LON: -1.31). From 1989 the site was divided  
718 into nine plots of c. 0.4 ha over which three contrasting grazing management practices  
719 (control, cattle and sheep) were randomly superimposed. These nine plots were  
720 monitored in June of each year from 1991-2009. More information: Woodcock et al.  
721 (2011).

722

723 **77.** The dataset is issued from an experiment located on a grassland in southeast  
724 Estonia (LAT: 58.11, and LON: 27.07). This dataset consists of 55 plots, where each  
725 plot was sampled an average of 8.9 times. The treatments were: fertilizer, sucrose and  
726 control. In each plot, the species cover (%) was visually estimated annually. More  
727 information: Liira et al. (2012).

728

729 **Figure Table S2.** Characteristics of the study sites.  
730

<b>ID</b>	<b>Country</b>	<b>Biome</b>	<b>Habitats</b>	<b>Duration</b>	<b>CP</b>	<b>MP</b>
1	USA	TGD	Grassland	12.5	NO	YES
2	USA	WS	Grassland	34.5	YES	YES
3	USA	TGD	Grassland	13.5	YES	YES
4	USA	SD	Grassland	11.2	YES	YES
5	USA	TGD	Savanna	21.5	YES	YES
6	USA	TGD	Grassland	8.0	YES	YES
7	USA	TGD	Grassland and Shrubland	11.5	YES	YES
8	South Africa	SD	Grassland	10.7	YES	NO
9	South Africa	SD	Savanna	15.8	YES	NO
10	South Africa	TGD	Savanna	14.7	YES	NO
11	South Africa	SD	Savanna	16.0	YES	NO
12	Hungary	WS	Savanna	14.5	YES	YES
13	USA	TF	Grassland	7.0	YES	YES
14	USA	TF	Savanna	6.2	YES	YES
15	USA	TF	Grassland	24.8	YES	NO
16	USA	TF	Grassland	22.0	YES	YES
17	USA	TF	Grassland	14.8	YES	YES
18	USA	TGD	Grassland	13.5	YES	YES
19	Germany	WS	Grassland	6.0	YES	NO
20	United Kingdom	WS	Shrubland	6.0	NO	YES
21	USA	TRF	Forest	21.4	YES	YES
22	Australia	SD and WS	Savanna	10.2	YES	NO
23	United Kingdom	WS	Grassland	8.0	YES	YES
24	France	WS	Grassland	28.0	NO	YES
25	Russia	BF	Grassland	24.3	YES	NO
26	United Kingdom	TF	Shrubland	12.0	YES	YES
27	USA	TF	Grassland	10.0	YES	NO
28	USA	TGD	Grassland	27.8	YES	NO
29	Czech Republic	TF	Grassland	16.8	YES	NO
30	Czech Republic	TF	Grassland	29.8	YES	NO
31	USA	WS	Grassland	18.9	YES	YES
32	Spain	WS	Grassland	12.0	YES	YES
33	USA	Tu	Grassland	6.0	YES	YES
34	USA	Tu	Grassland	6.0	YES	NO
35	Germany	WS	Grassland	7.7	YES	YES
36	Czech Republic	WS	Grassland	8.0	YES	NO
37	France	TF	Grassland	13.0	NO	YES
38	USA	TGD	Grassland	9.0	YES	YES
39	Czech Republic	WS	Grassland	16.0	YES	YES
40	France	WS	Grassland	8.0	YES	YES
41	USA	TGD	Grassland, Shrubland and Savanna	14.3	YES	NO
42	United Kingdom	TF	Grassland	6.8	YES	YES
43	United Kingdom	TF and TRF	Grassland	6.0	YES	YES

44	United Kingdom	TF	Grassland	7.0	YES	YES
45	United Kingdom	TF	Grassland	6.0	YES	YES
46	United Kingdom	TF	Shrubland	6.0	NO	YES
47	United Kingdom	TF	Savanna	6.0	YES	YES
48	Spain	BF	Grassland	19.0	YES	YES
49	Spain	TGD	Grassland	11.5	YES	NO
50	Spain	WS	Shrubland	17.0	YES	YES
51	USA	TGD	Grassland, Shrubland and Savanna	24.0	YES	NO
52	United Kingdom	TF	Savanna	6.0	NO	YES
53	United Kingdom	TF	Shrubland	10.0	YES	YES
54	United Kingdom	TF and WS	Grassland, Savanna and Forest	11.1	YES	NO
55	USA	TF	Forest	10.0	YES	NO
56	United Kingdom	WS	Grassland	9.9	YES	YES
57	Spain	TGD	Savanna	6.0	YES	YES
58	Germany	WS	Grassland	14.9	YES	NO
59	Germany	WS	Grassland	38.0	NO	YES
60	Switzerland	BF	Grassland and Forest	12.2	NO	YES
61	USA	TGD	Savanna	9.8	YES	YES
62	USA	TGD	Grassland, Shrubland and Savanna	9.2	YES	YES
63	USA	TGD	Grassland	7.7	YES	YES
64	USA	TGD	Forest	13.0	YES	NO
65	USA	TGD	Grassland and Savanna	16.4	YES	YES
66	USA	TGD	Grassland and Shrubland	8.2	YES	NO
67	Germany	WS	Forest	18.0	YES	YES
68	Czech Republic	WS	Grassland	10.3	YES	YES
69	Netherlands	WS	Grassland	28.9	NO	YES
70	China	WS	Grassland	9.0	YES	YES
71	Germany	WS	Salt marsh	18.7	YES	YES
72	Kenya	WS	Savanna	14.7	NO	YES
73	Norway	TRF	Grassland	6.0	NO	YES
74	USA	BF	Grassland and Savanna	12.0	YES	NO
75	Mongolia	TGD	Grassland	7.1	YES	YES
76	United Kingdom	WS	Grassland	18.0	NO	YES
77	Estonia	WS	Grassland	8.9	YES	YES

731

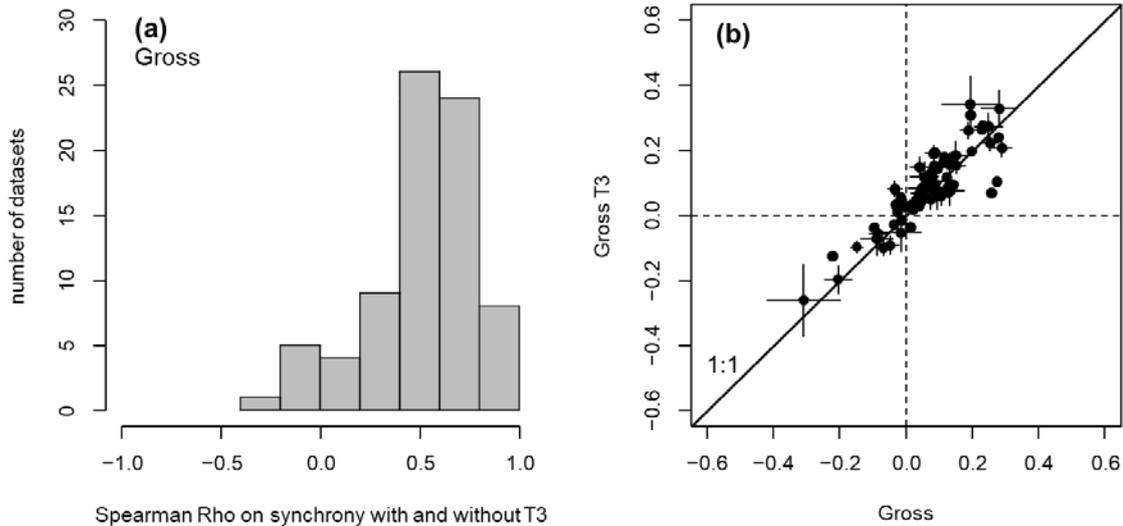
732 ID: Identification of the data set, biomes (TGD: temperate grassland desert, SD:  
733 subtropical desert, WS: woodland shrubland, TF: temperate forest, BF: boreal forest,  
734 Tu: Tundra, and TRF: temperate rain forest), Duration: Average number of years of  
735 the dataset, CP: presence of plots where the long-term conditions prior to the  
736 establishment of the sampling scheme were maintained throughout the sampling, MP:  
737 presence of plots exposed to different treatments that altered the long-term conditions.

738 Supporting Information to the paper  
 739 Valencia et al. Directional trends in species composition over time can lead to a  
 740 widespread overestimation of asynchrony. *Journal of Vegetation Science*.

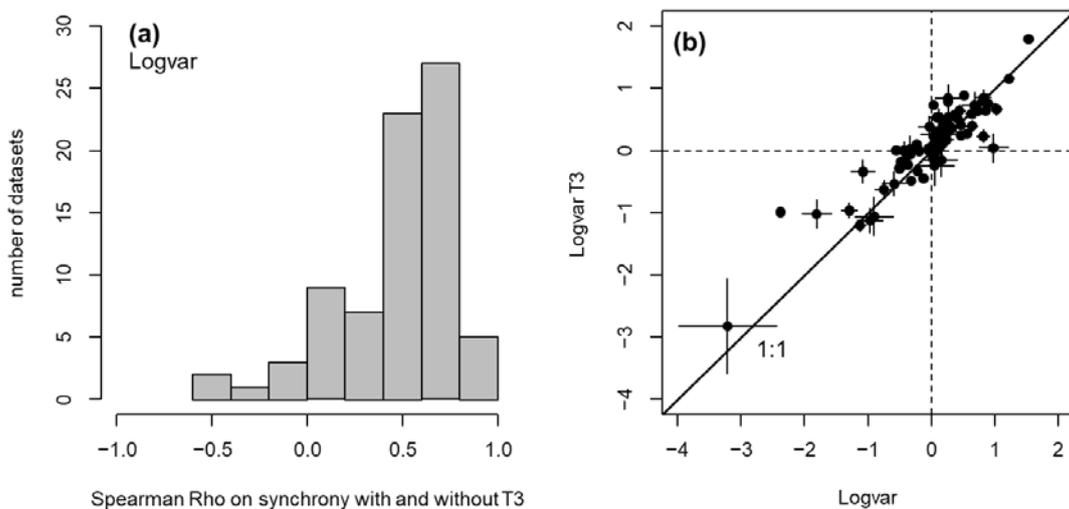
741  
 742 **Appendix S3.** Application of the analyses shown in Fig. 1 of the main text to the  
 743 three remaining indices of synchrony.

744  
 745 **Gross**

746 Note: on panel (b) the mean synchrony values with the T3 approach per datasets are  
 747 significantly higher than without the T3 approach ( $p < 0.001$ , paired t-test)  
 748



749  
 750  
 751 **Logvar**  
 752 Note: on panel (b) the mean synchrony values with the T3 approach per datasets are  
 753 significantly higher than without the T3 approach ( $p < 0.06$ , paired t-test)  
 754

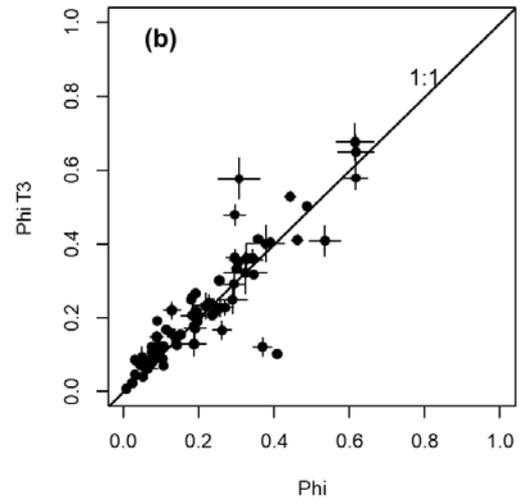
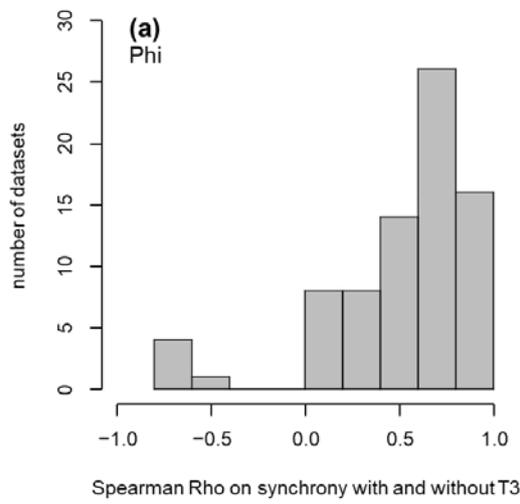


755  
 756  
 757

758  
759  
760  
761

**Phi**

Note: on panel (b) the mean synchrony values with the T3 approach per datasets are significantly higher than without the T3 approach ( $p < 0.22$ , paired t-test)

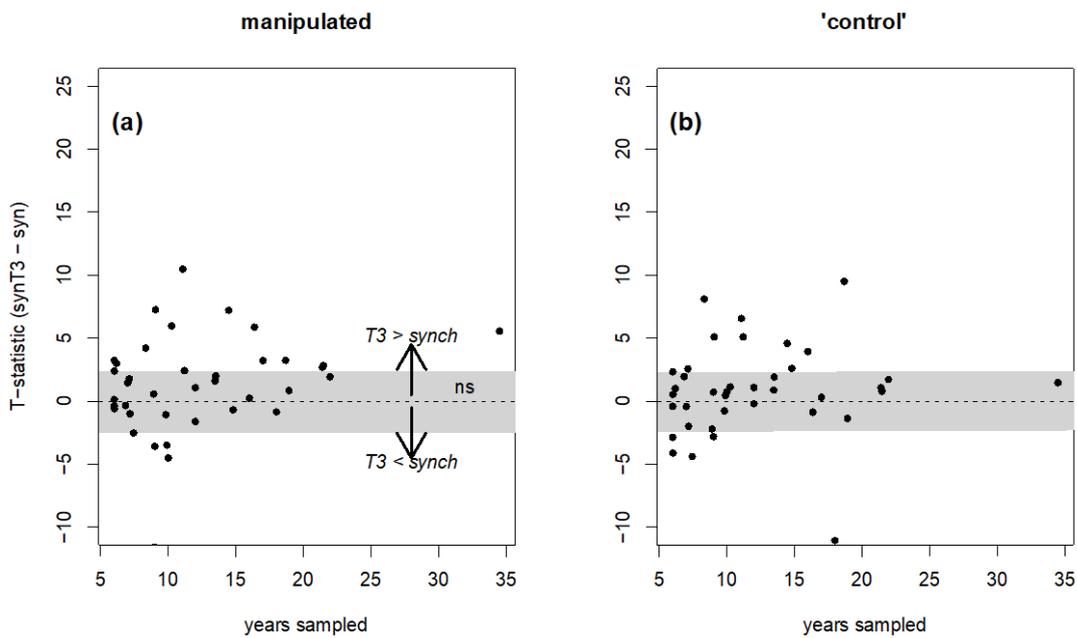


762

763 Supporting Information to the paper  
 764 Valencia et al. Directional trends in species composition over time can lead to a  
 765 widespread overestimation of asynchrony. *Journal of Vegetation Science*.  
 766

767 **Appendix S4.** Application of the analyses shown in Fig. 3 of the main text to the  
 768 three remaining indices of synchrony. For each index, also, a table of number of  
 769 datasets with either positive or negative significant t-statistic values is reported for  
 770 both manipulated and control plots (positive means that the T3 approach increased  
 771 synchrony; negative means that the T3 approach decreased synchrony). The grey area  
 772 in each panel reports and approximate are where t-statistic values were not significant  
 773 ('ns').  
 774

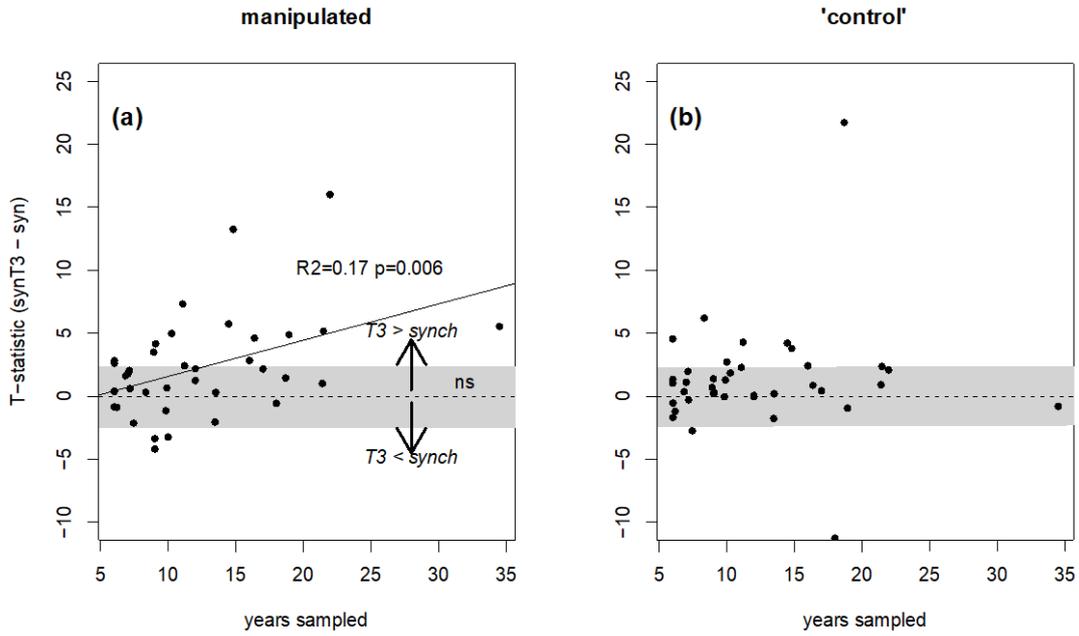
775 **Gross**



776  
 777  
 778  
 779  
 780  
 781  
 782  
 783

Manipulated		Control	
-	+	-	+
5	13	2	9

784 **Logvar**  
785

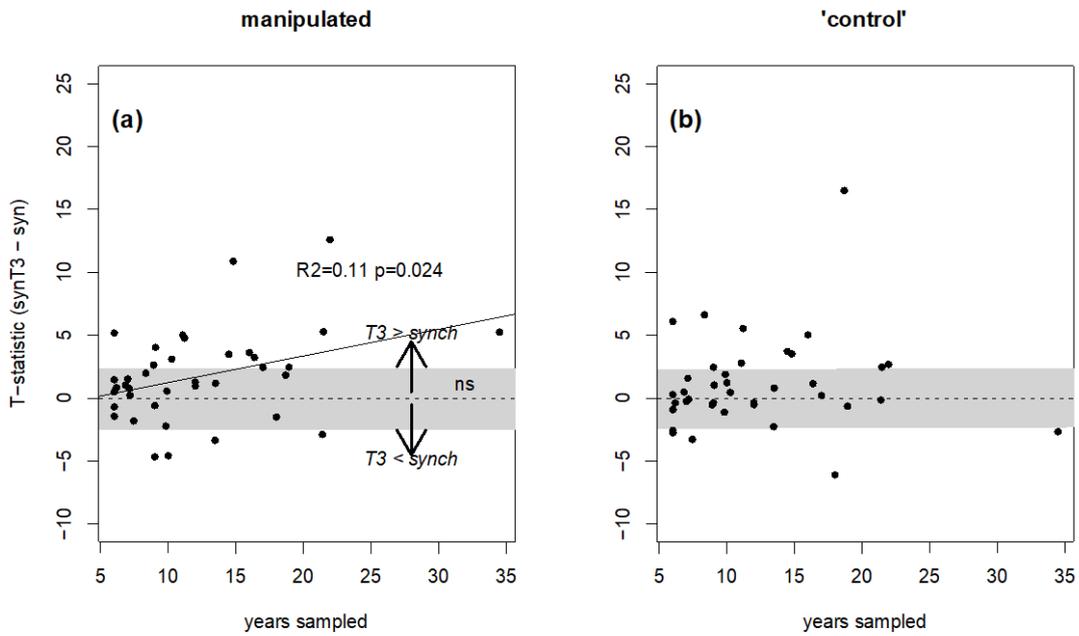


786

Manipulated		Control	
-	+	-	+
4	13	2	7

787  
788  
789

**Phi**



790  
791

Manipulated		Control	
-	+	-	+
5	14	3	8

792

793 Supporting Information to the paper

794 Valencia et al. Directional trends in species composition over time can lead to a

795 widespread overestimation of asynchrony. *Journal of Vegetation Science*.

796

797

798 **Appendix S5.** Results of the correlation between synchrony indices with species  
799 richness or with the CV of total abundance. Each table reports the number of datasets  
800 with a significant correlations between either Synchrony ~ richness or CV~richness  
801 (after correction for false discovery rates, see main text). The number of positive  
802 correlations is provided in parenthesis.

803

804

**Gross**

	Richness ~ synchrony	CV~synchrony
Without T3	11 (+7)	42 (+42)
With T3	13 (+8)	48 (+42)

805

806

**Logvar**

	Richness ~ synchrony	CV~synchrony
Without T3	21 (17)	52 (+52)
With T3	16 (13)	59 (+59)

807

808

**Phi**

	Richness ~ synchrony	CV~ synchrony
Without T3	31 (1)	66 (+66)
With T3	30 (1)	65 (65)

809

810 **References and Notes**

811

- 812 Bernhardt-Römermann, M., Römermann, C., Sperlich, S., & Schmidt, W. 2011.  
813 Explaining grassland biomass - the contribution of climate, species and  
814 functional diversity depends on fertilization and mowing frequency. *Journal of*  
815 *Applied Ecology*, 48: 1088–1097.
- 816 Blüthgen, N., Simons, N.K., Jung, K., Prati, D., Renner, S.C., Boch, S., Fischer, M.,  
817 Hölzel, N., Klaus, V.H., Kleinebecker, T., Tschapka, M., Weisser, W.W., &  
818 Gossner, M.M. 2016. Land use imperils plant and animal community stability  
819 through changes in asynchrony rather than diversity. *Nature Communications* 7:  
820 10697.
- 821 Braun-Blanquet, J., Brunies, S., Campell, E., Frey, E., Jenny H., Meylan, C., &  
822 Pallmann, H. 1931. Vegetations-Entwicklung im schweizerischen Nationalpark:  
823 Ergebnisse der Untersuchung von Dauerbeobachtungsflächen. *J.*  
824 *Naturforschenden Gesellschaft Graubünden*, 69: 4–82.
- 825 Chollet, S., Rambal, S., Fayolle, A., Hubert, D., Foulquié, D., & Garnier, E. 2014.  
826 Combined effects of climate, resource availability, and plant traits on biomass  
827 produced in a Mediterranean rangeland. *Ecology*, 95: 737–748.
- 828 Common, T., Wright, I., & Grant, S. 1998. The effect of grazing by cattle on animal  
829 performance and floristic composition in *Nardus*-dominated swards. *Grass and*  
830 *Forage Science*, 53: 260–269.
- 831 Crawley, M.J., Johnston, A.E., Silvertown, J., Dodd, M., Mazancourt, C. de, Heard,  
832 M.S., ... Edwards, G.R. 2005. Determinants of Species Richness in the Park  
833 Grass Experiment. *The American Naturalist*, 165: 179–192.
- 834 Day, F. 2016. Long-term N-fertilized vegetation plots on Hog Island, Virginia Coastal  
835 Barrier Islands, 1992–2014. Virginia Coast Reserve Long-Term Ecological  
836 Research Project.
- 837 Dornelas, M., Antão, L.H., Moyes, F., Bates, A.E., Magurran, A.E., Adam, D., ...  
838 Zettler, M.L. 2018. BioTIME: A database of biodiversity time series for the  
839 Anthropocene. *Global Ecology and Biogeography*, 27: 760–786.
- 840 Fernandez-Going, B.M., Anacker, B.L., & Harrison, S.P. 2012. Temporal variability  
841 in California grasslands: soil type and species functional traits mediate response  
842 to precipitation. *Ecology*, 93: 2104–2114.
- 843 Garnier, E., Fayolle, A., Navas, M.-L., Damgaard, C., Cruz, P., Hubert, D., ... Violle,

844 C. 2018. Plant demographic and functional responses to management  
845 intensification: A long-term study in a Mediterranean rangeland (R. Salguero-  
846 Gómez, Ed.). *Journal of Ecology*, 106: 1363–1376.

847 Gazol, A., Uria-Diez, J., Elustondo, D., Garrigó, J., & Ibáñez, R. 2016. Fertilization  
848 triggers 11 yr of changes in community assembly in Mediterranean grassland (S.  
849 Bartha, Ed.). *Journal of Vegetation Science*, 27: 728–738.

850 Grant, K., Kreyling, J., Beierkuhnlein, C., & Jentsch, A. 2017. Importance of  
851 Seasonality for the Response of a Mesic Temperate Grassland to Increased  
852 Precipitation Variability and Warming. *Ecosystems*, 20: 1454–1467.

853 Grant, S.A., Torvell, L., Common, T.G., Sim, E.M., & Small, J.L. 1996. Controlled  
854 grazing studies on *Molinia* grassland: effects of different seasonal patterns and  
855 levels of defoliation on *Molinia* growth and responses of swards to controlled  
856 grazing by cattle. *Journal of Applied Ecology*, 33: 1267–1280.

857 Grant, S.A., Torvell, L., Sim, E.M., Small, J.L., & Armstrong, R.H. 1996. Controlled  
858 grazing studies on *Nardus* grassland: effects of between-tussock sward height  
859 and species of grazer on *Nardus* utilization and floristic composition in two  
860 fields in Scotland. *Journal of Applied Ecology*, 33: 1053–1064.

861 Gross, K., Cardinale, B.J., Fox, J.W., Gonzalez, A., Loreau, M., Wayne Polley, H.,  
862 Reich, P.B., & van Ruijven, J. 2014. Species richness and the temporal stability  
863 of biomass production: a new analysis of recent biodiversity experiments. *The*  
864 *American Naturalist* 183: 1–12.

865 Harrison, S. 1999. Native and alien species diversity at the local and regional scales in  
866 a grazed California grassland. *Oecologia*, 121: 99–106.

867 Herben, T., Krahulec, F., Hadincová, V., Pecháčková, S., & Kováčiová, M. 1997.  
868 Fine-scale spatio-temporal patterns in a mountain grassland: do species replace  
869 each other in a regular fashion? *Journal of Vegetation Science*, 8: 217–224.

870 Herben, T., Mayerová, H., Skálová, H., Hadincová, V., Pecháčková, S., & Krahulec,  
871 F. 2017. Long-term time series of legume cycles in a semi-natural montane  
872 grassland: evidence for nitrogen-driven grass dynamics? (R. Ostertag, Ed.).  
873 *Functional Ecology*, 31: 1430–1440.

874 Hulme, P.D., Merrell, B.G., Torvell, L., Fisher, J.M., Small, J.L., & Pakeman, R.J.  
875 2002. Rehabilitation of degraded *Calluna vulgaris* (L.) Hull-dominated wet heath  
876 by controlled sheep grazing. *Biological Conservation*, 107: 351–363.

877 Hulme, P.D., Pakeman, R.J., Torvell, L., Fisher, J.M., & Gordon, I.J. 1999. The

878 effects of controlled sheep grazing on the dynamics of upland *Agrostis-Festuca*  
879 grassland. *Journal of Applied Ecology*, 36: 886–900.

880 Jürgens, N., Schmiedel, U., & Hoffman, M. 2010. *Biodiversity in southern Africa*.  
881 Göttingen & Windhoek: Klaus Hess.

882 Kertész, M., Aszalós, R., Lengyel, A., & Ónodi, G. 2017. Synergistic effects of the  
883 components of global change: Increased vegetation dynamics in open, forest-  
884 steppe grasslands driven by wildfires and year-to-year precipitation differences  
885 (M. Heydari, Ed.). *PLOS ONE*, 12: e0188260.

886 Lepš, J. 2014. Scale- and time-dependent effects of fertilization, mowing and  
887 dominant removal on a grassland community during a 15-year experiment (S.  
888 Wan, Ed.). *Journal of Applied Ecology*, 51: 978–987.

889 Lepš, J., Götzenberger, L., Valencia, E., & de Bello, F. 2019. Accounting for long-  
890 term directional trends on year-to-year synchrony in species fluctuations.  
891 *Ecography*. doi: 10.1111/ecog.04528

892 Lepš, J., Májerková, M., Vítová, A., Doležal, J., & de Bello, F. 2018. Stabilizing  
893 effects in temporal fluctuations: management, traits, and species richness in high-  
894 diversity communities. *Ecology*, 99: 360–371.

895 Liira, J., Ingerpuu, N., Kalamees, R., Moora, M., Pärtel, M., Püssa, K., ... Zobel, M.  
896 2012. Grassland diversity under changing productivity and the underlying  
897 mechanisms - results of a 10-yr experiment (M. Huston, Ed.). *Journal of*  
898 *Vegetation Science*, 23: 919–930.

899 Londo, G. 1976. The decimal scale for relevés of permanent quadrats. *Vegetatio*, 33:  
900 61–64.

901 Loreau, M., & de Mazancourt, C. 2008. Species synchrony and its drivers: neutral and  
902 nonneutral community dynamics in fluctuating environments. *The American*  
903 *Naturalist* 172: E48–E66.

904 Louault, F., Pottier, J., Note, P., Vile, D., Soussana, J.-F., & Carrère, P. 2017.  
905 Complex plant community responses to modifications of disturbance and nutrient  
906 availability in productive permanent grasslands (H. H. Bruun, Ed.). *Journal of*  
907 *Vegetation Science*, 28: 538–549.

908 Marriott, C.A., Bolton, G.R., Barthram, G.T., Fisher, J.M., & Hood, K. 2002. Early  
909 changes in species composition of upland sown grassland under extensive  
910 grazing management. *Applied Vegetation Science*, 5: 87–98.

911 Onipchenko, V.G., Semenova, G. V., & Maarel, E. 1998. Population strategies in

- 912 severe environments: alpine plants in the northwestern Caucasus. *Journal of*  
 913 *Vegetation Science*, 9: 27–40.
- 914 Pakeman, R.J., Hulme, P.D., Torvell, L., & Fisher, J.M. 2003. Rehabilitation of  
 915 degraded dry heather [*Calluna vulgaris* (L.) Hull] moorland by controlled sheep  
 916 grazing. *Biological Conservation*, 114: 389–400.
- 917 Pakeman, R.J., & Nolan, A.J. 2009. Setting sustainable grazing levels for heather  
 918 moorland: a multi-site analysis. *Journal of Applied Ecology*, 46: 363–368.
- 919 Pardo, I., Doak, D.F., García-González, R., Gómez, D., & García, M.B. 2015. Long-  
 920 term response of plant communities to herbivore exclusion at high elevation  
 921 grasslands. *Biodiversity and Conservation*, 24: 3033–3047.
- 922 Rennie, S., Adamson, J., Anderson, R., Andrews, C., Bater, J., Bayfield, N., ...  
 923 Whittaker, M. 2016. UK Environmental Change Network (ECN) coarse grain  
 924 vegetation data: 1993-2012. *NERC Environmental Information Data Centre*.
- 925 Rothacher, J.S. 2013. Soil Moisture and vegetation cover patterns after logging and  
 926 burning an old-growth Douglas-fir forest in the Andrews Experimental Forest,  
 927 1960-1983. *Environmental Data Initiative*.
- 928 Rueda, M., Rebollo, S., & García-Salgado, G. 2013. Contrasting impacts of different-  
 929 sized herbivores on species richness of Mediterranean annual pastures differing  
 930 in primary productivity. *Oecologia*, 172: 449–459.
- 931 Schmidt, W. 2006. Biodiversity and plant productivity in grassland succession: the  
 932 effects of nutrient levels and disturbance regime. *Polish Botanical Studies*, 22:  
 933 437–448.
- 934 Schmidt, W. 2009. Vegetation. In Brumme, R. & Khanna, P.K. (eds.), *Functioning*  
 935 *and Management of European Beech Ecosystems*, pp. 65–86. Springer, Berlin.
- 936 Schmidt, W. 2007. Wie rasch kehrt die Vielfalt in artenarme Wiesenfuchsschwanz-  
 937 Wiesen zurück?– Ergebnisse aus Dauerflächenuntersuchungen zur  
 938 Extensivierung des Grünlandes. *Hercynia-Ökologie und Umwelt in Mitteleuropa*,  
 939 40: 111–132.
- 940 Schuhmacher, O., & Dengler, J. 2013. *Das Land-Reitgras als Problemart auf*  
 941 *Trockenrasen. Handlungsempfehlungen zur Reduktion von Calamagrostis*  
 942 *epigejos. Ergebnisse aus einem Praxisversuch*. NABU Hamburg, Hamburg,  
 943 Germany, Hamburg, Germany.
- 944 Schütz, M., Krüsi, B., & Edwards, P. 2000. Succession research in the Swiss National  
 945 Park: From Braun-Blanquet's Permanent Plots to Models of Long-term

946 Ecological Change. *Nationalpark-Forschung in der Schweiz*, 89: 289.

947 Šmilauer, P., & Šmilauerová, M. 2013. Asymmetric relationship between grasses and  
948 forbs: results from a field experiment under nutrient limitation. *Grass and*  
949 *Forage Science*, 68: 186–198.

950 Song, M.H., Yu, F.H., Ouyang, H., Cao, G.M., Xu, X.L., & Cornelissen, J.H.C. 2012.  
951 Different inter-annual responses to availability and form of nitrogen explain  
952 species coexistence in an alpine meadow community after release from grazing.  
953 *Global Change Biology*, 18: 3100–3111.

954 Stapp, P. 2013. SGS-LTER Long-Term Monitoring Project: Vegetation Cover on  
955 Small Mammal Trapping Webs on the Central Plains Experimental Range,  
956 Nunn, Colorado, USA 1999 -2006, ARS Study Number 118. *Environmental*  
957 *Data Initiative*.

958 Tinney, F., Aamodt, O., & Journal, H. 1937. Preliminary report of a study on methods  
959 used in botanical analyses of pasture swards. *Agronomy journal*, 29: 835–840.

960 Vandvik, V., Heegaard, E., Maren, I., & Aarrestad, P. 2005. Managing heterogeneity:  
961 the importance of grazing and environmental variation on post-fire succession in  
962 heathlands. *Journal of Applied Ecology*, 42: 139–149.

963 Veblen, K.E., Porensky, L.M., Riginos, C., & Young, T.P. 2016. Are cattle surrogate  
964 wildlife? Savanna plant community composition explained by total herbivory  
965 more than herbivore type. *Ecological Applications*, 26: 1610–1623.

966 Viereck L.A., Van Cleve, K., Chapin, F.S., Hollingsworth, T.N., & Ruess, R.W. 2010.  
967 Vegetation Plots of the Bonanza Creek LTER Control Plots: Species Percent  
968 Cover (1975 - 2009). *Environmental Data Initiative*.

969 Wesche, K., Ronnenberg, K., Retzer, V., & Miede, G. 2010. Effects of large herbivore  
970 exclusion on southern Mongolian desert steppes. *Acta Oecologica*, 36: 234–241.

971 Woodcock, B.A., McDonald, A.W., & Pywell, R.F. 2011. Can long-term floodplain  
972 meadow recreation replicate species composition and functional characteristics  
973 of target grasslands? *Journal of Applied Ecology*, 48: 1070–1078.

974