

1 **Damping and lag effects of precipitation variability across trophic levels in Uruguayan**
2 **rangelands**

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28 Abstract

29 Extensive livestock production is one of the activities that, without requiring habitat
30 conversion, contributes to grassland conservation and human well-being. In Uruguay,
31 approximately 60% of the land is covered by natural temperate grasslands, which are entirely
32 devoted to extensive livestock production, mainly cattle and sheep. In this study we described
33 the spatial and temporal variability of aboveground net primary productivity (ANPP), net
34 secondary productivity (NSP) and trophic efficiency (TEf) of temperate grasslands in two
35 geomorphological regions of Uruguay (Basaltic “Cuesta” and Eastern Hills), and explored their
36 relationship with the mean and annual precipitation (MAP and PPT, respectively). Specifically,
37 we asked whether Uruguayan grasslands are able to damp precipitation variability at the levels
38 of vegetation and herbivores. Additionally, we searched for lag effects of precipitation on
39 primary and secondary productivity. The study period included seven growing seasons, from
40 2005 to 2012. PPT, ANPP and NSP were calculated monthly for 32 sections (administrative
41 units) of both regions, and aggregated at the growing season level. NSP-related data included
42 not only livestock numbers, but also livestock births, mortality and transportation, as well as
43 milk and wool production. ANPP showed a clear inter-regional difference, the Eastern Hills
44 region was more productive ($69814 \text{ MJ}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$) than the Basaltic “Cuesta” ($60762 \text{ MJ}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$).
45 NSP showed no inter-regional differences (742 vs. 754 $\text{MJ}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$, respectively) and TEf was
46 higher in Basaltic “Cuesta” (0.0125) than in Eastern Hills (0.0107). As expected, ANPP was
47 strongly determined by the amount of rainfall, both in space and time. Although we did not
48 find a relationship between current year NSP and ANPP, secondary productivity was positively
49 related with PPT and ANPP with a two-year lag in Basaltic “Cuesta”. Also, we found that the
50 interannual variabilities of ANPP and NSP were, respectively, 60 and 40% lower than the
51 variability of precipitation, but contrary to our expectations, NSP was 40% more variable than
52 ANPP. Only 1.17% of the energy captured by grasslands in Uruguay is converted into domestic
53 herbivore production, a value close to the average reported for other grasslands and savannas.

54 *Keywords: Livestock systems, Aboveground Net Primary Productivity, Net Secondary*
55 *Productivity, Trophic Efficiency, interannual variability.*

56 1. Introduction

57 Extensive livestock production is one of the activities that, without requiring habitat
58 conversion, contributes to both grassland conservation and human well-being, through the
59 supply of provision and regulation ecosystem services (Sala and Paruelo, 1997; Heidenreich,
60 2009). Compared to alternative land uses of temperate grasslands, ranching minimize the
61 Human Appropriation of Net Primary Production (NPP) (Baeza and Paruelo, 2018) and, hence,
62 maximize C sequestration (Caride et al., 2012). In general, the production objective of livestock
63 systems based on natural grasslands is to optimize the harvest of net secondary productivity
64 (NSP) (Briske and Heitschmidt, 1991) which, in turn, is often limited by the rate of
65 accumulation of aboveground biomass, or aboveground net primary productivity (ANPP)
66 (McNaughton et al., 1989; Oesterheld et al., 1998). Grasslands' ANPP is nearly the only source
67 of energy for extensive livestock production systems at the global scale. Since grasslands are
68 recognized as the most endangered biome in the world (Carbutt et al., 2017), the ability of
69 these systems to optimize NSP yield through time is relevant to both grassland conservation
70 and economic sustainability (Kemp and Michalk, 2007).

71

72 In natural grasslands, abiotic and biotic controls of ANPP (Paruelo et al., 1999; Epstein et al.,
73 2006) set limits on the energy available to herbivores (McNaughton et al., 1989). For a range of
74 Mean Annual Precipitation (MAP) between 200 and 1200 mm, the spatial variation in mean
75 ANPP among sites is positively and linearly associated with MAP ("spatial model", Sala et al.,
76 1988; Paruelo et al., 1999; 2010). For a given site, ANPP temporal variation shows a lower
77 degree of association with annual precipitation (PPT) and lower slopes (or Precipitation
78 Marginal Response $\text{gC}\cdot\text{ha}^{-1}\cdot\text{mm}^{-1}$; Verón et al., 2005) at both extremes of the regional gradient
79 than that of the spatial model ("temporal model", Sala and Lauenroth, 1992; Paruelo et al.,
80 1999). Part of the variability not explained by the PPT is associated with biogeochemical and
81 vegetation constraints (Epstein et al., 2006), the disturbance regime (Oesterheld et al., 1999)
82 or lag effects (Oesterheld et al., 2001).

83

84 NPP correlates with a number of descriptors of the structure and functioning of the herbivore
85 trophic level. McNaughton et al. (1989) showed that, for natural systems and among sites,
86 herbivore biomass, consumption and NSP increased with primary productivity. Animal
87 husbandry has a large effect on herbivore biomass. Agricultural systems can support 6 times
88 more herbivore biomass than natural systems given the same ANPP, reflecting the influence of

89 energy subsidies in the form of different management actions (Oesterheld et al., 1992).
90 Interestingly, the log-log relationship between herbivore biomass and ANPP had a slope
91 greater than 1 for both types of systems, indicating a more-than-proportional increase in
92 herbivore biomass per unit change in ANPP.

93

94 Trophic efficiency ($TEf = NSP/NPP$) represents the proportion of plant production transformed
95 into animal products (Lindeman, 1942; Chapin et al., 2011). While NSP directly reflects the
96 magnitude of benefits obtained in extensive livestock systems, trophic efficiency relativizes
97 those benefits to available resources. Following Irisarri et al. (2014), TEf can be decomposed
98 into consumption efficiency and production efficiency which represent, respectively, the
99 proportion of NPP (commonly expressed as ANPP) consumed by herbivores, and the
100 proportion of such consumption transformed into NSP. Although the latter has been broadly
101 studied in intensive livestock production systems (Shelton, 1998; Cantalapiedra-Hilar, 2018),
102 the difficulty in obtaining accurate data on forage consumption by grazing herbivores
103 (Greenwood et al., 2016) has limited research on rangeland-livestock trophic efficiency to very
104 few studies. Irisarri et al. (2014) studied how the TEf of commercial ranches changed across an
105 ANPP gradient in temperate and subtropical rangelands of Argentina. Their results showed low
106 TEf at both extremes of the gradient and maxima for intermediate values.

107

108 Herbivore energy requirements vary over time, mainly in cow-calf systems, with maximum
109 requirements at the end of gestation and during lactation (National Research Council, 2000;
110 2007). Thus, the temporal synchrony between forage supply and demand is a major
111 determinant of the consumption efficiency (Briske and Heitschmidt, 1991). ANPP presents
112 seasonal fluctuations (Baeza et al., 2010; Guido et al., 2014) that cannot be fully matched by
113 domestic herbivores requirements. Consequently, (in absence of feed supplementation)
114 annual NSP is often determined by the ANPP of the least productive part of the year,
115 generating temporal forage surpluses that, to the extent that they cannot be transferred,
116 determine an important reduction in trophic efficiency (Briske and Heitschmidt, 1991;
117 McNaughton et al., 1991). For semiarid rangelands of Africa, with large spatial and temporal
118 variation in forage, it has been proposed that herbivore populations are regulated by the
119 limited forage available in key resource areas (e.g. drainage lines, sumps, dambos) during the
120 dry season (Illius and O'Connor 1999; Fynn, 2012). On the other hand, behavioral and
121 physiologic traits allow ruminants to adapt to resource variability by transferring energy

122 through time in their biomass (Atti et al., 2004; Blanc et al., 2006), but such adaptive ability
123 would be impaired at relatively high and fixed stocking rates, like those that often occur in
124 livestock systems (Do Carmo et al., 2016).

125

126 The Río de la Plata Grasslands is one of the most extensive areas of temperate grasslands on
127 the planet (Soriano, 1992; Paruelo et al., 2007; Oyarzabal et al., 2020). Uruguay is entirely
128 included in this biome, and approximately 60% of its surface is currently covered by natural
129 temperate grasslands (DIEA, 2011; Baeza and Paruelo, 2020). This area is entirely devoted to
130 extensive livestock production. Uruguay's livestock systems, traditionally based on natural
131 grasslands and mixed grazing of cattle and sheep, are organized almost exclusively on private
132 ranches, with commercial purposes (Pereira, 2003; Berretta, 2003). Depending on the region,
133 the relative proportion of sheep and cattle varies, as well as the structure of herds and flocks
134 (DIEA, 2008, 2010, 2015, Panario, 2016). Due to the expansion of agriculture and afforestation,
135 livestock systems in Uruguay experienced an increase in stock density per unit of rangeland
136 area (2.65% for the period 1990-2000; Paruelo et al., 2006). Additionally, an intensification
137 process that includes the increase of perennial and annual fodder crops, grain
138 supplementation, and confined fattening systems, took place (Bervejillo, 2013; Modernel et
139 al., 2016). However, these changes predominated in areas with deeper and more fertile soils.
140 Most of the livestock production in the Basaltic "Cuesta" and Eastern Hills areas (Fig. 1) is
141 based on the forage provided by natural grasslands (DIEA, 2015; Altesor et al., 2019).

142

143 Various studies described the spatial and temporal variability of ANPP in Uruguayan
144 grasslands, both from field biomass harvesting (Altesor et al., 2005; Pezzani et al., 2017) and
145 through the use of remote sensing techniques (Baeza et al., 2010; Guido et al., 2014; Gallego
146 et al., 2017; Texeira et al., 2019). In turn, a number of studies evaluated, in the Rio de la Plata
147 Grasslands, the relationship between ANPP and livestock density, both at the level of the
148 entire biome and locally (Oesterheld et al., 1992, 1998; Soca et al., 2011; Irisarri et al., 2014;
149 Irisarri and Oesterheld, 2020). Bervejillo (2013) described the spatial and temporal variability
150 of cattle NSP for the geomorphological regions of Uruguay. However, the spatial and temporal
151 variability of trophic efficiency, as well as its relationship with MAP and PPT, is unknown for
152 Uruguayan grasslands.

153

154 Droughts are a major disturbance in livestock systems (Diaz-Solis et al., 2009). In the Rio de la
155 Plata Grasslands, precipitation tends to be higher than normal during El Niño events, while
156 during La Niña events, precipitation is lower than normal (INUMET, 2019). In Uruguay, summer
157 (January-March) accumulated precipitation may range between 154 (1989) and 365 mm
158 (2010). Such variation determines changes in primary productivity (Paruelo et al., 1999) which,
159 in turn, impact on livestock production (Diaz-Solis et al., 2006). Such impact, that may even
160 include livestock mortality, usually cause a drastic reduction in reproductive performance,
161 hence determining lag effects of droughts events on NSP.

162

163 In several grasslands from North and South America, ANPP is less variable than annual
164 precipitation (Paruelo and Lauenroth, 1998; Durante et al., 2017; Irisarri et al., 2019). Such
165 response may result, mainly in the driest grasslands, from a constraint imposed by the
166 vegetation structure (abundance of life forms, species composition) on ANPP, which confines
167 its variability between certain limits. In addition, soil water storage and plant physiological
168 adjustments may reduce the effect of drought years on ANPP. Humid or subhumid grasslands,
169 on the other hand, experience constraints related to resource availability (N or light) that
170 reduce their response to hydric conditions. Furthermore, most livestock systems operate in
171 enclosed areas where several human interventions, like water provision, disease and predator
172 control and changes in livestock categories, help to maintain animal numbers. As a result, the
173 density of herbivores is partially decoupled from ANPP fluctuations, and lower interannual
174 variability of NSP -compared to ANPP- is expected. This pattern was observed for several
175 rangelands from USA and Argentina (Irisarri et al., 2019; Irisarri and Oesterheld, 2020).
176 According with these precedents, we expect that the coefficient of variation (CV) of PPT > CV
177 ANPP > CV NSP.

178

179 In this article we characterized the spatial and temporal variability of ANPP, NSP and Tef within
180 and between two geomorphological regions (Basaltic “Cuesta” and Eastern Hills) of Uruguay.
181 We evaluated the relationship of these three descriptors of C dynamics with both MAP (spatial
182 models) and PPT (temporal models), exploring the occurrence of lag effects. Finally, we
183 evaluated the existence of amplification and/or damping effects of precipitation variability at
184 the plant and herbivore trophic levels.

185

186 2. Materials and methods

2.1. Study areas

The Uruguayan territory is entirely included in the Campos region of the Rio de la Plata Grasslands. Our study focused on two out of nine geomorphological units of the country: the Basaltic “Cuesta” and the Eastern Hills (Panario et al., 2015) (Fig. 1). The Basaltic “Cuesta” region, located in the North, covers approximately 4.4 million hectares (25% of the territory). Shallow soils restricted agricultural and forestry development, making the Basaltic “Cuesta” the area with the greatest predominance of natural grasslands in Uruguay (DIEA, 2000, 2011). Lezama et al. (2019) identified two grassland communities in the region: Sparsely-vegetated grasslands of the Basaltic “Cuesta” (*Selaginella sellowii-Rostraria cristata* community), characterized by meso-xerophytic species, and densely-vegetated grasslands of the Basaltic “Cuesta” (*Steinchisma hians-Piptochaetium stipoides* community), dominated by mesophytic species.

The Eastern Hills region consists of a set of elevations with a SW-NE direction and the maximum height range of the Uruguayan territory. It occupies 2.5 million hectares and comprises a wide variety of geological substrata (ectinites, migmatites, granites, among others) (Bossi and Navarro, 1988). Medium-depth soils prevail in the region, followed by shallow and rocky soils (Altamirano et al., 1976; Panario, 2016). Grasslands of the Eastern Hills correspond to three phytosociological communities (Lezama et al., 2019): sparsely-vegetated grasslands of Eastern Hills, North Eastern Sedimentary Basin and the South Central region (*Trachypogon spicatus-Crocianthemum brasiliense* community), dominated by meso-xerophytic species; densely-vegetated grasslands of the Eastern Hills, North Eastern Sedimentary Basin and the South Central region (*Eryngium horridum-Juncus capillaceus* community), dominated by mesophytic species; and tall and densely-vegetated grasslands of the Eastern Hills, North Eastern Sedimentary Basin and the South Central region (*Chascolytrum poomorphum-Paspalum pumilum* community) which comprise dense stands with a high stratum of tall grasses (*Paspalum quadrifarium*, *Andropogon lateralis* or *Erianthus angustifolius*), and is characterized by mesophytic and hygrophytic species. The woody component (shrubs, isolated trees and forest patches) is common in the Eastern Hills region.

The climate in both geomorphological regions is temperate subtropical, with an average annual temperature of 17.5°C, varying between 16 and 19°C, and an average annual precipitation of 1350 mm (INUMET, 2019).

221 Even though cattle and sheep ranching is the main economic activity in both geomorphological
222 units (DIEA, 2000, 2011), there are differences in the livestock systems of each region. While
223 cow-calf systems predominate in the Eastern Hills, the Basaltic “Cuesta” has a higher
224 proportion of sheep and a higher heterogeneity in cattle production orientations, with higher
225 proportion of full-cycle and finishing systems than Eastern Hills (DIEA, 2008, 2010, 2015).

226

227 *2.2. Temporal and spatial resolution*

228

229 The study period included seven growing seasons (July-June) from 2005 to 2012. The spatial
230 resolution corresponded to an administrative unit of the “*Ministerio del Interior*” of Uruguay
231 (“*Secciones Policiales*”, hereafter SP or Sections). For the analysis, we selected those Sections
232 almost fully included (>90%) in the geomorphological regions, with an area of annual fodder
233 crops lower than 1%. A total of 19 sections were considered for the Basaltic “Cuesta”
234 (2.585.424 ha) and 13 for the Eastern Hills (1.123.371 ha) (Fig. 1). PPT, ANPP and NSP were
235 calculated monthly for the whole study period and aggregated at the growing season level.

236

237 *2.3. ANPP, NSP, TEf and Precipitation estimations*

238

239 The ANPP of the rangelands included in each section was derived from remotely sensed data
240 applying Monteith (1972) model (Eq. 1; Piñeiro et al., 2006; Grigera et al., 2007):

241

$$242 \text{ANPP} = \text{APAR} * \text{RUE} = \text{fAPAR} * \text{PARi} * \text{RUE} \quad (1)$$

243

244 Where APAR ($\text{MJ} \cdot \text{ha}^{-1} \cdot \text{d}^{-1}$) is the total amount of photosynthetically active radiation absorbed
245 by green vegetation, PARi ($\text{MJ} \cdot \text{ha}^{-1} \cdot \text{d}^{-1}$) is the incident photosynthetically active radiation,
246 fAPAR is the fraction of that radiation intercepted by green vegetation, and RUE (gMJ^{-1}) the
247 energy conversion coefficient of absorbed radiation into above-ground biomass.

248

249 fAPAR was estimated from the Enhanced Vegetation Index (EVI), derived from the MODIS
250 (Moderate Resolution Imaging Spectroradiometer, product MOD13Q1 collection 6) sensor on
251 board of the EOS Terra platform. We used a locally-calibrated equation ($\text{fAPAR} = 1.4914 * \text{EVI} -$
252 0.1382). MODIS images consist of a gridded 16-days composite with 250 m pixel size (~6 ha).
253 Each EVI image was filtered using its associated ‘per pixel’ quality image (Roy et al., 2002); only

254 those pixels without clouds or shadows and with low levels of aerosols in the atmosphere were
255 analysed. When a pixel did not have the highest quality, its value was discarded and replaced
256 by a simple linear interpolation of the previous and the following dates. Monthly fAPAR was
257 calculated using the weighted sum of the values from the MODIS images corresponding to a
258 particular month.

259

260 Incoming Photosynthetic Active Radiation (PAR_i; MJha⁻¹d⁻¹) was estimated for the entire
261 country, interpolating data from the weather stations of the “*Instituto Nacional de*
262 *Investigación Agropecuaria*” (INIA). We used a RUE constant value of 0.313 gMJ⁻¹, derived from
263 field calibrations performed on different grassland communities of Uruguay (Baeza et al., 2011;
264 Oyarzabal et al., 2011; Gallego et al., 2017; Paruelo et al., 2019). Pixels corresponding to each
265 section were averaged to derive monthly ANPP values (kgDM.ha⁻¹.m⁻¹). ANPP was converted
266 into energy units (MJ.ha⁻¹.m⁻¹) assuming an energy content of plant dry matter of 16.76
267 MJ.kgDM⁻¹ (used by Oesterheld et al., 1992 based on Golley, 1961).

268 The NSP was calculated as the sum of energy accumulated in the form of cattle and sheep
269 biomass (B), milk (M) and wool (W) (Eq. 2):

270

$$271 \text{NSP}_{\text{Tot}} = \text{NSP}_B + \text{NSP}_M + \text{NSP}_W \quad (2)$$

272

273 For its estimation, we used compiled data from the Annual Affidavit provided by ranchers to
274 the “*División Contralor de Semovientes*” (DICOSE) of the “*Ministerio de Ganadería Agricultura y*
275 *Pesca*” (MGAP, Uruguay) and from the Property and Transit Guides, provided by DICOSE. Such
276 data include not only livestock numbers but also livestock inputs and outputs at the Section
277 level. These include transportation to and from other SP, transportation to slaughter, livestock
278 consumption at ranch and mortality, allowing for calculation of all demographic fluxes, as well
279 as milk production. In such a way, our approach represents an improvement over those studies
280 that use only livestock numbers data and therefore estimate the demographic fluxes from
281 published average values. In the Supplementary Material 1 we present the main data used on
282 our study. Original data are available upon request from the corresponding author.

283 Monthly biomass production (NSP_B; MJ.ha⁻¹.m⁻¹; Eq. 3) of each species was calculated as:

284

$$285 \text{NSP}_B = (\text{BM}_{\text{exp}} - \text{BM}_{\text{imp}} + \text{BM}_f - \text{BM}_i) * \text{ha}^{-1} * 9.90 \quad (3)$$

286

287 Where BM_{exp} represents the biomass (in kg live weight) exported from the section; BM_{imp} , the
288 imported biomass; and BM_f and B_{mi} , the amount of biomass in the section at the end and
289 beginning of the month, respectively (for a detailed description of biomass-production
290 calculation, see Gutiérrez, 2016). We referred the data to the area of rangelands of the
291 section. The constant 9.90 is the caloric content of 1 kg live weight, expressed in MJ, and was
292 used to convert animal production into energy units (Coughenour et al., 1985).

293

294 Greasy-wool production (NSP_w) was estimated by adding up monthly values (calculated as a
295 function of body weight, considering flock structure) and converting the values integrated over
296 the growing season into energy, assuming constant fat and protein contents. Milk production
297 (NSP_m) was estimated by converting the values produced in the growing season into energy,
298 considering its monthly distribution and fat and protein composition (see Supplementary
299 Material 2 for more information).

300

301 Trophic efficiency (TEf) resulted from the NSP:ANPP ratio (Eq. 4):

302

$$303 \quad TEF = NSP \cdot ANPP^{-1} \quad (4)$$

304

305 Where ANPP and NSP represent the growing season values, calculated for both variables in
306 each section. As other study on TEf at regional scale (see Irisarri et al., 2014), we did not
307 convert ANPP into NPP because an arbitrary constant value was the only alternative, and this
308 may hide some spatial and/or temporal patterns.

309

310 Precipitation data were obtained from product 3b43 of the Tropical Rainfall Measuring Mission
311 (TRMM; <http://trmm.gsfc.nasa.gov/3b43.html>). This product provides monthly mean
312 precipitation data in mm/h with a spatial resolution of $0.25^\circ \times 0.25^\circ$ (25 x 25 km,
313 approximately) since 1998. The precipitation values provided by this product have been
314 contrasted with data from local meteorological stations, showing high adjustment (Teixeira et
315 al., 2015). The precipitation values were converted into accumulated monthly (mm/month)
316 and annual (mm/year) precipitation. Only pixels mostly included (> 70%) in the individual
317 Sections were used. If this condition was not met, the precipitation values of the pixels that
318 occupied the Section were averaged.

319

320 Mean ANPP, NSP and TEf of both regions were compared using *t*-tests. Normality and
321 homoscedasticity were evaluated prior to analysis. All data meet the assumptions required by
322 the *t*-test analysis. The relationships of ANPP, NSP and TEf with MAP (spatial models) and PPT
323 (temporal models) were analysed by simple linear regressions. For the spatial models, the 7-
324 year average of the variables in each section was considered. For the temporal analysis, we
325 used two types of spatial resolution: 1) average values per region (BC or EH) and 2) data per
326 section. We also evaluated lag effects regressing the variables on the PPT of previous years. To
327 evaluate damping or amplification effects, we correlated the interannual variability (described
328 by the coefficient of variation, CV) of precipitation and the interannual changes of the other
329 variables (ANPP, NSP, TEf). We also correlated the interannual variability of ANPP and NSP.

330

331 3. Results

332 3.1. *Spatial variability of ANPP, NSP and TEf*

333

334 ANPP showed a clear inter-regional difference (Fig. 1A): forage resources of all sections in
335 Eastern Hills were more productive than those of the Basaltic “Cuesta” sections (69814 vs
336 60762 MJ.ha⁻¹.y⁻¹; *t*= -16.108, *p*<0.001). Within the Basaltic “Cuesta”, ANPP increased towards
337 the NW and SE. No clear geographic pattern was observed in the Eastern Hills region. NSP, on
338 the other hand, showed no inter-regional differences (*t*= 0.4007, *p*=0.691), with an overlap of
339 the ranges of both regions (Fig. 1B). In the Basaltic “Cuesta”, NSP showed a similar spatial
340 pattern than ANPP, while for the Eastern Hills, NSP gradually decreased towards the North and
341 the South. ANPP and NSP variability between regions determined that the livestock production
342 systems of the Basaltic “Cuesta” were more efficient than those of the Eastern Hills (Fig. 1C; *t*=
343 4.4237, *p*<0.001). Within regions, variability of TEf was quite similar to the pattern observed
344 for NSP.

345

346 Fig. 1.

347

348 3.2. *Spatial models*

349

350 As observed in many grasslands all over the world, and despite of the relative low range of
351 MAP considered (less than 350 mm, corresponding to the wettest extreme of the MAP

352 gradient observed in grasslands areas), the spatial model fitted to the average ANPP and MAP
353 was significant with a positive slope ($r=0.472$; $n=32$; $p<0.01$; Fig. 2A). The slope of the model
354 was $25.9 \text{ MJ}\cdot\text{ha}^{-1}\cdot\text{mm}^{-1}$, equivalent to $1.54 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{mm}^{-1}$. The spatial models for both NSP and
355 TEf were not significant ($r=0.166$; $n=32$; $p=0.362$ and $r=0.148$; $n=32$; $p=0.418$, respectively) (Fig.
356 2B and 2C).

357

358

Fig. 2.

359

360 3.3. Temporal models

361 Considering the whole dataset, ANPP and PPT showed a positive correlation ($r=0.89$; $n=14$; p
362 <0.01). The correlation was higher for those sections corresponding to the Basaltic “Cuesta”
363 ($r=0.89$; $n=7$; $p<0.01$) than those of the Eastern Hills ($r=0.69$; $n=7$; $p=0.08$) (Fig. 3A). As
364 expected, the slope of the temporal model was lower than for the spatial model (15.6 vs 25.9).
365 The slopes for the Basaltic “Cuesta” and Eastern Hills databases were quite similar (15.1 vs
366 14.6, respectively). The two regions differed in the Y-intercept of the models, being higher for
367 the Eastern Hills. The temporal model for NSP was not significant ($r=0.27$; $n=7$; $p=0.549$), and
368 significant with a negative slope for TEf ($r=0.93$; $n=7$; $p<0.01$) (Fig. 3B and 3C).

369

370 Within each section (the highest spatial resolution of the analysis), annual PPT explained a
371 great proportion of ANPP interannual variability (Fig. 4A; for 66% of the sections r was greater
372 than 0.75 and significant, $p<0.05$). For NSP, the association with annual PPT was either positive
373 or negative, with a central tendency close to zero. In two of the sections, the association was
374 statistically significant and occurred at the positive and negative extremes of the distribution
375 (Fig. 4B). Finally, TEf correlations also presented both positive and negative values; however, a
376 high proportion of the sections showed negative values and 25% were significant (Fig. 4C). This
377 is the consequence of an increase of ANPP with annual PPT but either a decrease or no change
378 in NSP with PPT over time and within each section. For both regional datasets, TEf presented a
379 significant negative relationship with current year precipitation (Fig. 3C).

380

381

Fig. 3.

382

383

Fig. 4.

384

385 We explored the existence of lag effects on the temporal models (Table 1). NSP showed a
386 significant positive relationship with both PPT and ANPP with a lag of two years in the Basaltic
387 “Cuesta” region. In the Eastern Hills region, we did not find significant lag effects. Lag-effects at
388 the individual section level are shown in the Supplementary Material 3.

389

390

Table 1

391

392 *3.4. Changes in variability across trophic levels*

393 Average interannual variability, assessed through the coefficient of variation (CV), was 10% for
394 the ANPP, 14% for the NSP and 16% for the TEf. In turn, PPT CV was 24% (Fig. 5). The
395 interannual variability of the three variables was not related to the interannual variability of
396 precipitation, meaning that the most or least variable sections in PPT were not necessarily the
397 most/least variable in terms of ANPP, NSP or TEf. As shown by the position of the data points
398 below the 1:1 line of Fig. 5A, all sections were less variable in ANPP than in precipitation. The
399 NSP was also less variable than precipitation (Fig. 5B) but was actually more variable than the
400 ANPP (Fig. 5D). TEf showed greater variability than ANPP and NSP, but less than precipitation
401 (Fig. 5C).

402

403

Fig. 5.

404

405 4. Discussion

406

407 This study describes, for the first time, the spatial and temporal variability of the trophic
408 efficiency (NSP/ANPP) of extensive grazing production systems of Uruguay. For its estimation,
409 we used a detailed database which allowed us to calculate NSP. We also complement other
410 studies on temperate rangelands, providing evidence about damping effects of precipitation

411 variability at the levels of vegetation and herbivores, as well as delayed effects of precipitation
412 on secondary productivity.

413

414 As expected, ANPP was strongly determined by the amount of rainfall (Sala et al., 1988;
415 Paruelo et al., 1999; 2010). Both in space (among sections) and time (across years for a given
416 site), ANPP showed a positive relationship with mean annual precipitation and current year
417 precipitation, respectively. The slope of our spatial model was similar to that reported in a
418 previous study, for the same range of mean annual precipitation (1.54 vs 1.79 kg. ha⁻¹.mm⁻¹ in
419 Paruelo et al., 2010). As expected, the slope values for a relative low precipitation range are
420 lower than those observed covering large gradients (i.e. Sala et al., 1988; Paruelo et al., 1999).
421 The slopes of the temporal models were consistently lower than those of the spatial models
422 (ratio = 0.6). Durante et al. (2016) also reported substantially lower slopes for the temporal
423 than for the spatial model, for lowlands grasslands and uplands pastures of the Argentinean
424 Pampas. The ratio between the slopes of the temporal and spatial models in our study is
425 higher than expected according to the double logistic model proposed by Paruelo et al. (1999)
426 for temperate grasslands worldwide. The difference between the slopes of the spatial and
427 temporal models reflects the influence of biogeochemical (the restrictions imposed by other
428 resources, i.e. light or N) or vegetational (differences in relative growth rate of dominant
429 species) constraints at the site level (Epstein et al., 2006; Oyarzabal et al., 2008).

430

431 We did not find, though, a relationship between current year NSP and ANPP. Indeed, NSP was
432 negatively associated with PPT (the main control of ANPP) in several sections, although in only
433 one was significant. The lack of a significant relationship between NSP and PPT or ANPP may
434 be due to limitations in the calculation of NSP, where constant individual weight gains –for
435 each given livestock category and age- were assumed. This approach underestimates the
436 spatial and interannual variability of weight gain, thus resulting in NSP variability
437 underestimations. However, we identified interesting lags on the response of NSP to changes
438 in both ANPP and PPT in the Basaltic “Cuesta” region. NSP correlated with ANPP with a two-
439 year lag. This suggests that the impact of above- and below-average rainfall years, in terms of
440 ANPP, would translate into NSP two years later. Management practices aimed to maximize
441 forage intake per area, i.e. high stocking rates, may compromise the performance of calves in
442 subsequent years by determining low weight at weaning (Viñoles et al., 2013). Thus, the
443 impact of drought on forage availability would be rather reflected on subsequent productive

444 performance than on current mortality. The possibility to detect lag effects in this study was
445 enhanced by the account of actual yearly livestock inputs and outputs that the database
446 compile allowed. Some factors, like mortality or livestock exports aimed to reduce stocking
447 rate, might respond to ANPP variability in shorter time intervals than others, like births or
448 broodstock recruitment. The sole use of livestock numbers for calculating NSP results in
449 rougher estimations, because it cannot fully account for the temporal variability of those
450 demographic fluxes.

451

452 The trophic efficiency of Uruguayan extensive livestock production systems based on natural
453 grasslands was, in average, 1.17%. This value of TEf is close to the average value reported by
454 Irisarri et al. (2014) for grasslands and savannas in Argentina. Due to the resolution of our
455 analysis, the range of TEf among the sections studied was lower (0.76-1.47%) than those
456 observed by Irisarri et al. (2014) at the farm level for the same range of ANPP (approx. 0.4-
457 2.4%). The trophic efficiency observed in our study represents an animal production (including
458 meat, wool and milk) equivalent to 19.8 kg of meat per ton of forage DM produced.

459

460 TEf was lower in the Eastern Hills than in the Basaltic “Cuesta”. These regions differ in the
461 relative importance of woody components, both at the landscape (small forest patches
462 associated to azonal environments) and patch levels (shrubs and isolated trees in grassland
463 areas). Baeza et al. (2019) reported that native forest patches occupy 3.1% of the Basaltic
464 “Cuesta” while the percentage is 8.1 in the Eastern Hills. Gallego et al. (2020) showed that
465 woody encroachment is a common process on grasslands of the Eastern Hills, and that the
466 presence of shrubs and small trees increases ANPP and reduces its variability. The woody
467 component would be responsible of the higher Y-intercept of the ANPP-PPT model fitted for
468 the Eastern Hills area. However, woody plants concentrate productivity in unpalatable items,
469 reducing the consumption efficiency (Anadón et al., 2014). These authors found a density
470 reduction of 1.6 reproductive cows per square kilometre for each 1% increase in tree cover, in
471 high-productivity areas of Argentina. Also, Irisarri et al. (2014) suggest that the reduction of
472 consumption efficiency, observed at both extremes of an ANPP gradient in Argentina
473 rangelands, is due to changes in the proportion of plant functional types and, in consequence,
474 forage quality.

475

476 The structure of herds can also determine differences in consumption efficiency. The diversity
477 of ruminants would increase efficiency through the complementarity of their grazing patterns
478 (Vallentine, 2001). Thus, the greater equity in the proportion of cattle and sheep biomass in
479 the Basaltic “Cuesta” could also explain the greater trophic efficiency in that region. In
480 addition, higher sheep/cattle ratio could increase efficiency in the Basaltic “Cuesta” by
481 increasing the contribution of wool to the NSP (15% vs. 9% for BC and EH, respectively; see
482 Supplementary Material 1), as fiber production is less variable than meat production, even in
483 harsh conditions like droughts (Easdale et al., 2014). Irisarri et al. (2014) observed greater
484 efficiencies in the use of the energy consumed in Patagonian wool systems than in cattle-
485 dominated systems in sub-humid and sub-tropical pastures in Argentina, attributing them, in
486 part, to the type of product obtained. Finally, the cattle production system could partly
487 account for the observed differences in Tef. In Eastern Hills, reproduction-oriented (or ‘cow-
488 calf’) systems contribute more to NSP than in Basaltic “Cuesta” (22% vs. 15% of weaned calves
489 production, respectively; see Supplementary Material 1). Cow-calf systems need to sustain
490 high-biomass individuals (cows) that provide little return (0.7 calves/year), making this system
491 energetically more expensive (i.e. higher respiratory costs) than systems oriented to fattening
492 livestock in preparation for slaughter.

493

494 For both regions, Tef varied negatively with PPT, reflecting the influence of rainfall on ANPP,
495 the input term of the ratio. An increase in the abundance of the resource (water, in this case),
496 increased ANPP but did not translate proportionally into NSP. Differences in the temporal
497 response of processes determining C dynamics at the plant and herbivore trophic levels, as
498 shown by the existence of lag effects on the NSP-ANPP relationship, may account for the
499 negative response of Tef to PPT.

500

501 The interannual variability of ANPP was lower than that of precipitation. This damping effect
502 was also observed by Durante et al. (2016) for grasslands of the Flooding Pampa. Several
503 mechanisms may account for this effect. Soil may act as a capacitor in hydric terms, providing
504 water to plants in periods of no rainfall. In extreme cases, as in Patagonia steppes, with a more
505 seasonal precipitation pattern than the Rio de la Plata Grasslands (Paruelo et al., 2007), most
506 of the water evapotranspired during the growing season is accumulated during winter (Paruelo
507 and Sala, 1995). Of course, vegetation in itself may also account for this effect, through
508 drought tolerance or avoidance mechanisms.

509

510 Even though the CV of NSP was still lower than the PPT CV, NSP variability was greater than
511 that of ANPP. This amplification effect may be responsible for the public impact of drought
512 events on the Uruguayan economy: the effects of changes in the availability of forage are
513 amplified at the level of the marketable product. The mechanisms of such increase in
514 variability at the herbivore trophic level may relate, again, to diverse factors. Livestock and
515 grassland management is clearly critical in determining the response of NSP. In North
516 American grasslands, beef productivity was more variable than ANPP at high stocking-rates,
517 while damping effects occurred at lower stocking rates (Irisarri et al., 2019), suggesting the
518 existence of density-dependent tipping points in NSP variability, that would be important to
519 determine. Also, changes in the seasonal distribution of ANPP may cause a decoupling
520 between forage supply and herds nutritional demands, which in turn, may contribute to
521 amplify the variability at the herbivore trophic level. In Basaltic “Cuesta” and Eastern Hills, the
522 highest interannual ANPP variability was observed in summer months (Baeza et al., 2010;
523 Guido et al., 2014), in synchrony with cattle’s breeding season peak (Pereira, 2003). Resource
524 variability at these critical moments -affecting reproductive performance- may widen NSP
525 variability, as observed in all sections of Eastern Hills, where cow-calf systems predominate. In
526 both regions, the inability to balance resource variability has been attributed to high stocking
527 rates and low forage allowances (Modernel et al., 2019). Moreover, forage allowance (ratio of
528 forage mass and animal body weight per unit area, Allen et al., 2011) and sward structure
529 affects daily forage intake by cattle (Jamieson and Hodgson 1979; da Trindade et al., 2016).
530 Sward structure is determined by the conservation status of grassland patches (Altesor et al.,
531 2019), as well as by short-term grazing management decisions (stock density, timing of grazing,
532 rest periods, etc.). In such a way, two grassland areas may have a similar ANPP but quite
533 different sward structure which, in turn, determine differences in DM intake and, hence, on
534 NSP. Finally, the detection of amplifying effects could also be due to the feasibility for NSP
535 estimation (this study) or measurement (Irisarri et al., 2019), compared to the use of herbivore
536 biomass as its surrogate.

537

538 A backcasting exercise (Kanter et al., 2016) carried out in Uruguay, suggested that beef
539 production can be increased by at least 25% in 15 years using production targets which can be
540 combined with the already existing and validated technologies to increase rates of pregnancy
541 and weaning and to reduce average slaughter age. For the geomorphological regions studied,

542 this would imply an increase of NSP from around 75 to 94 kg.ha⁻¹.y⁻¹ and, in turn, average TEF
543 to 1.44%. Although the goal is quite challenging, this value was reached in at least one of the
544 sections analysed and is within the range of TEF reported at the farm level by Irisarri et al.,
545 (2014).

546

547 5. Conclusions

548 Only 1.17% of the energy captured by grasslands in Uruguay is converted into domestic
549 herbivore production. Our study, though, provided an underestimation of trophic efficiency,
550 because non-domestic herbivores were not considered. Managed grasslands ecosystems were
551 able to damp annual resources (rainfall) variability, but such damping effect occurred at the
552 plant trophic level, since the variability of ANPP was amplified at the herbivore trophic level.
553 We found lag effects of precipitation on NSP, at least for one of the studied areas. Such lag
554 effects suggest that the changes in forage resources impact more on demographic variables of
555 longer-term response, such as reproductive parameters. The possibility to estimate NSP,
556 instead of using herbivore biomass as a surrogate, may be critical for detecting those effects.

557

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943 Tables

944 Table 1. Lag effects on the temporal models for the Basaltic “Cuesta” and Eastern Hills regions.

945 PPT-1; ANPP-1 and PPT-2; ANPP-2: 1-year lag and 2-year lag, respectively.

		Basaltic “Cuesta”				Eastern Hills		
		<i>n</i>	<i>r</i>	R ²	<i>p</i>	<i>r</i>	R ²	<i>P</i>
	PPT	7	0.893	0.797	0.007	0.693	0.481	0.084
ANPP	PPT-1	6	-0.628	0.394	0.182	-0.685	0.470	0.133
	PPT-2	5	0.042	0.002	0.947	-0.078	0.006	0.901
	PPT	7	-0.229	0.052	0.622	-0.105	0.011	0.824
	PPT-1	6	-0.701	0.491	0.121	-0.143	0.020	0.788
NSP	PPT-2	5	0.946	0.895	0.015	0.218	0.047	0.725
	ANPP	7	-0.075	0.006	0.874	0.429	0.184	0.337
	ANPP-1	6	-0.769	0.592	0.074	0.094	0.009	0.860
	ANPP-2	5	0.981	0.963	0.003	0.417	0.174	0.485
	PPT	7	-0.808	0.653	0.028	-0.799	0.639	0.031
TEf	PPT-1	6	0.235	0.055	0.654	0.551	0.304	0.257
	PPT-2	5	0.452	0.204	0.445	0.214	0.046	0.729

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958 Figure captions

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960 Fig. 1. Spatial distribution of the ANPP (A), NSP (B) and TEf (C) of the livestock systems in the
961 Basaltic “Cuesta” (BC) and Eastern Hills (EH) regions, Uruguay. The boxplots show the median
962 and 25th and 75th percentiles of the 3 variables for the period 2005 – 2012. (*) indicate
963 significant differences between regions ($p < 0.001$) according to a *t*-test performed on the
964 means.

965

966 Fig. 2. Spatial models showing the relationship between ANPP (A); NSP (B) and TEf (C) and
967 Mean Annual Precipitation (MAP). Points represent sections from Basaltic “Cuesta” (black
968 dots) and Eastern Hills (white dots). Solid line: general model; Dotted lines: regional models.

969

970 Fig. 3. Temporal models showing the relationship between ANPP (A); NSP (B) and TEf (C) and
971 Annual Precipitation (PPT) for 7 growing seasons in Basaltic “Cuesta” (black dots) and Eastern
972 Hills (white dots). Solid line: general model; Dotted lines: regional models.

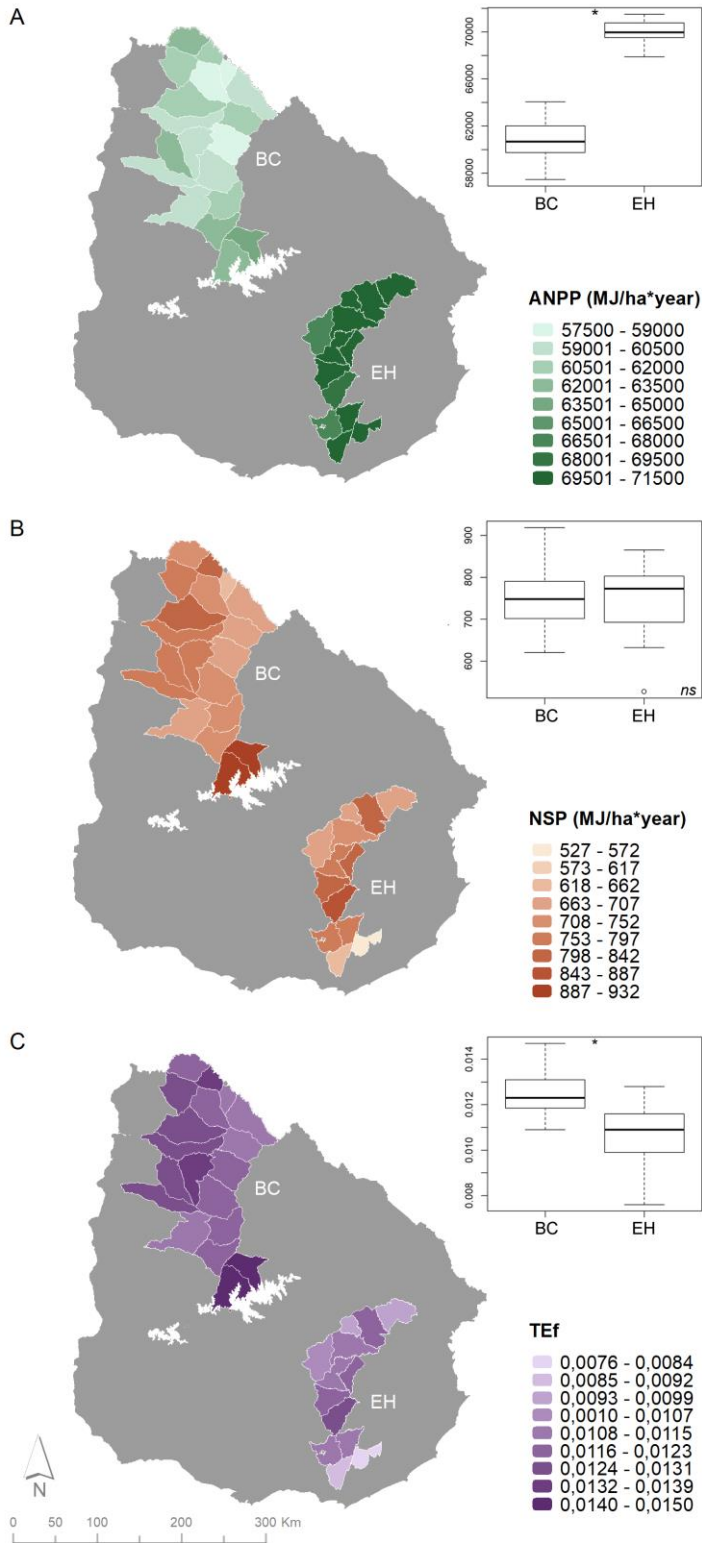
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974 Fig. 4. Distribution of standardized slopes (Pearson correlation coefficients) of the relationship
975 between ANPP (A), NSP (B) and TEf (C), and Annual Precipitation (PPT) of 19 Sections of
976 Basaltic “Cuesta” and 13 sections of Eastern Hills. Asterisks indicate significant correlations.

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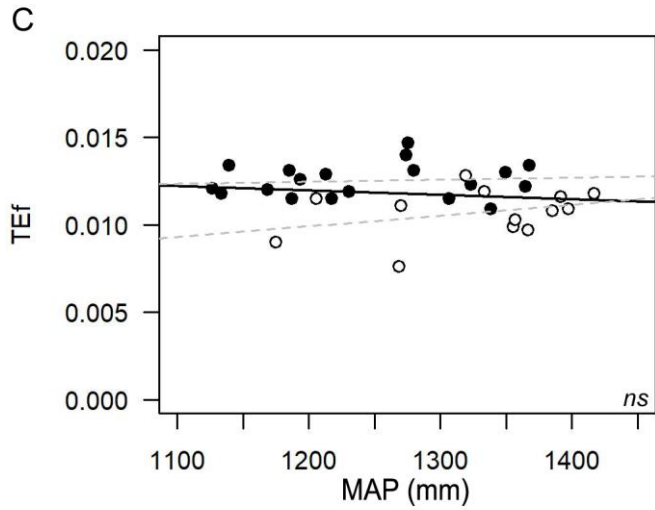
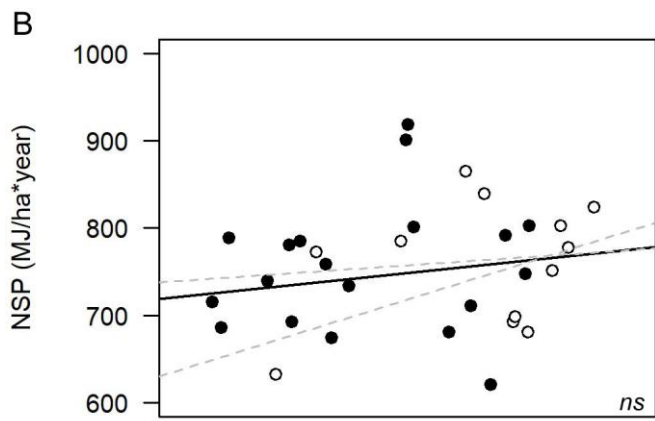
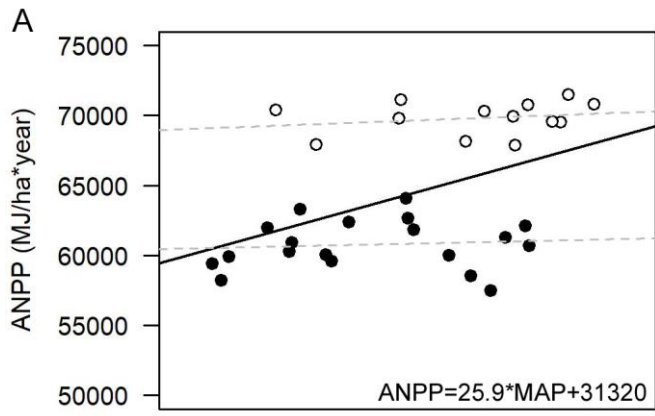
978 Fig. 5. Relationship between the interannual variability (CV) of ANPP (A), NSP (B) and TEf (C),
979 and the interannual variability of precipitation for Sections of the Basaltic “Cuesta” (black dots)
980 and Eastern Hills (white dots) regions. (D) Relationship between the interannual variability of
981 NSP and the interannual variability of ANPP. The solid line represents the 1:1 relation. The
982 dotted lines correspond to the mean and the maximum and minimum values of the variables.

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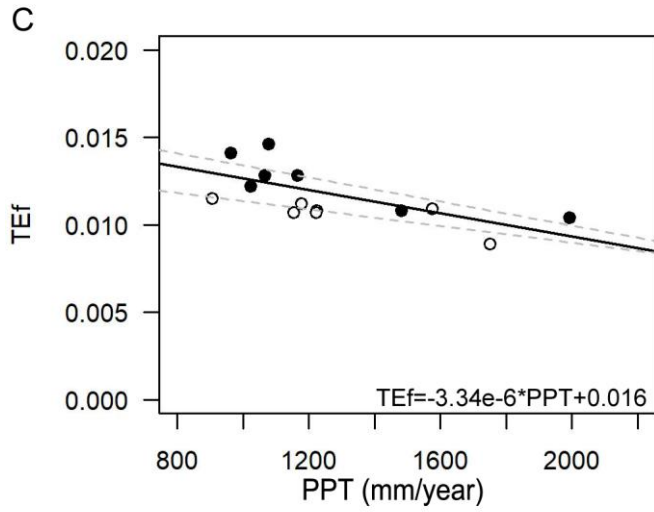
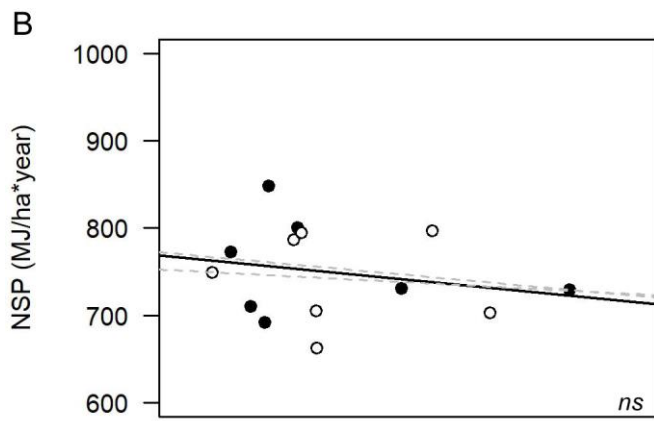
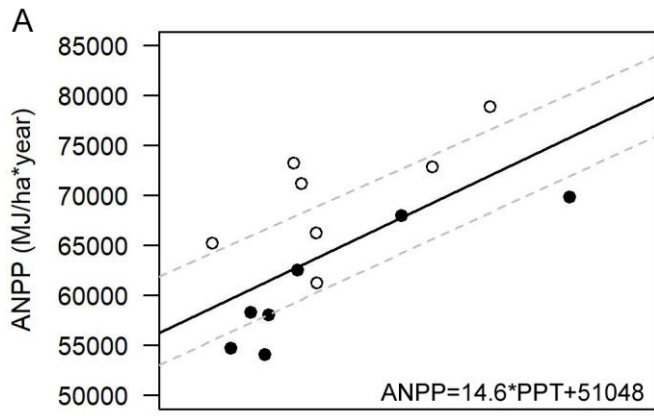
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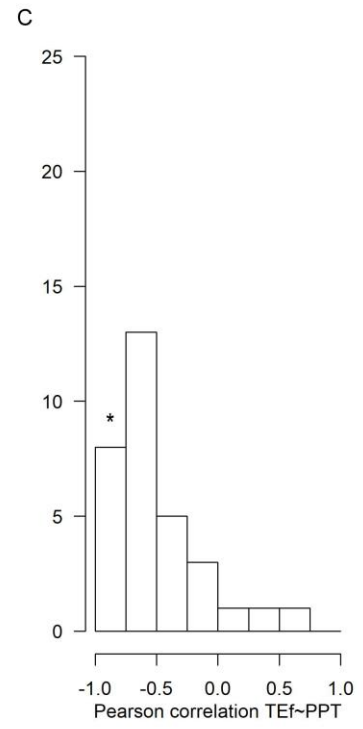
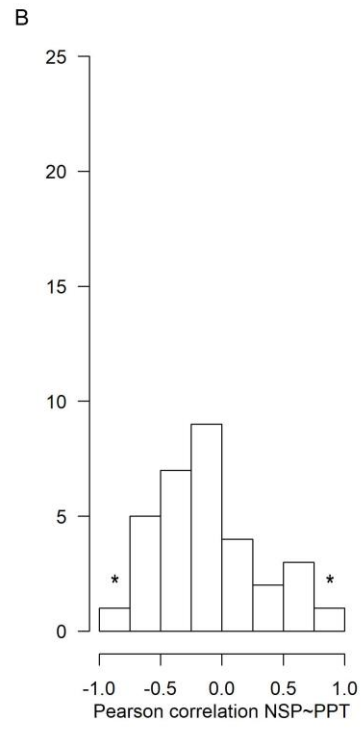
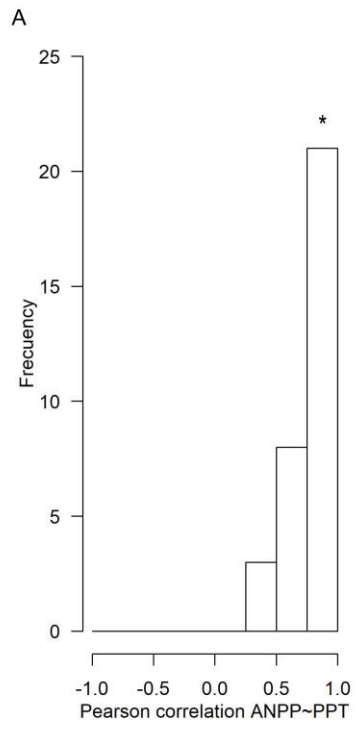
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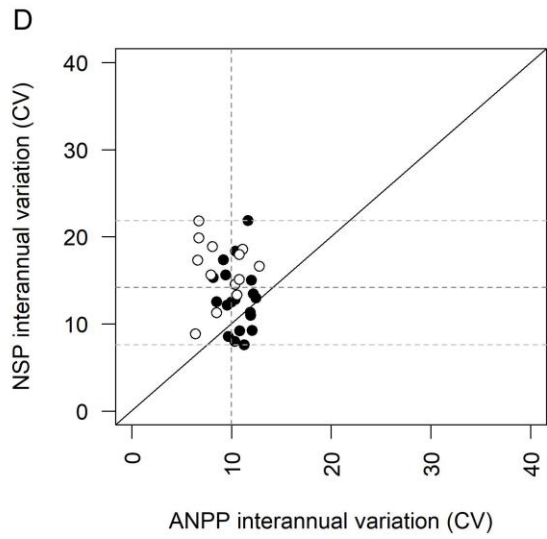
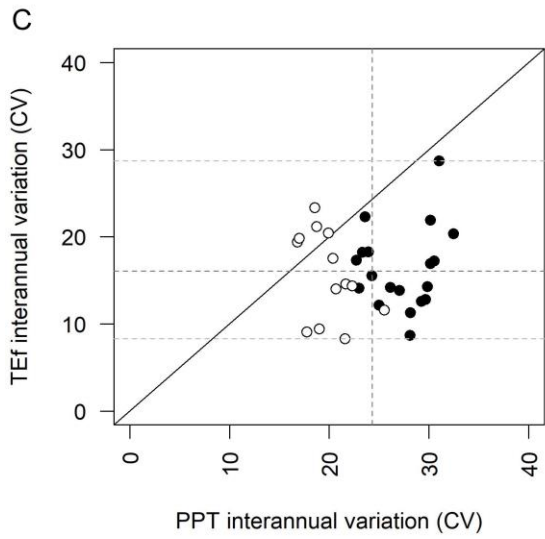
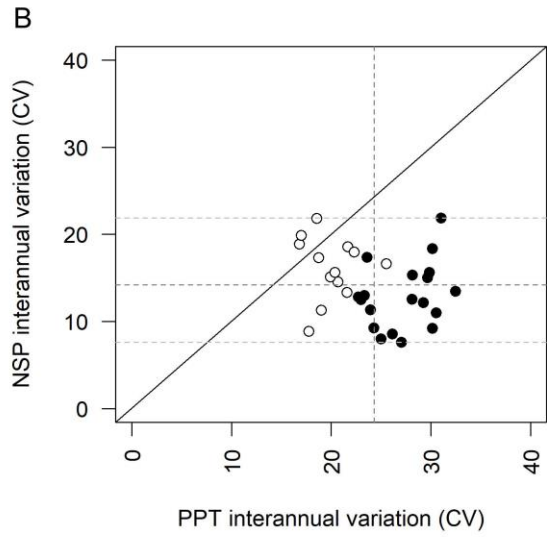
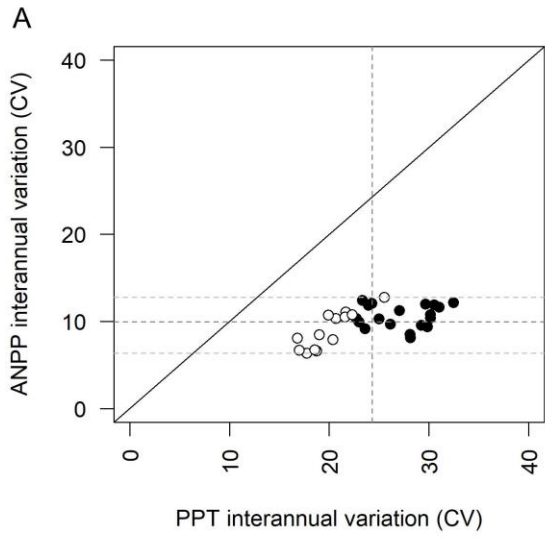
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